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Comparative Anatomy of Japanese Cyatheaceae

Contributions to Cytology and Genetics from the Departments of Plant-Morphology and of Genetics, Botanical Institute, Faculty of Science, Tokyo Imperial University, No. 59

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With 74 Text-Figures

I. Introductory and Historical

The Cyatheaceae include nearly all tree-ferns, and are mostly tropical with a wide geological range. They may be classified into three tribes and seven genera as is shown in the following key.[1]

Cyatheaceae—Sori globose or oblong. Indusium present or absent. Receptaculum mostly present. Sporangia numerous, sessile or stalked. Annulus complete, sometimes incomplete with a small stomium; oblique. Stem usually dendroid.

A. Sori marginal. Indusium bivalvular. Annulus incomplete with a small stomium. . . . . (I) DICKSONIEAE
- a. Fertile pinnae mostly unmodified. Last pinna not equilateral. Stem subterranean. . . . . (1) *Balantium* (3 sp.)
- b. Fertile pinnae mostly unmodified. Last pinna equilateral. Stem erect. . . . . (2) *Dicksonia* (12 sp.)
- c. Fertile pinnae modified. Stem dendroid. . (3) *Cibotium* (8 sp.)

B. Sori marginal. Indusium spherical with terminal opening. Annulus homologous. . . . . (II) THYRSOPTERIDEAE
(4) *Thyrsopteris* (1 sp.)

1) Modified and abbreviated from DIELS in ENGLER & PRANTL's Pflanzenfamilien, 1902. The number of species of each genus is given in parentheses. According to CHRISTENSEN's Index Filicum (1906), it is as follows: *Balantium* 3 sp., *Dicksonia* 17 sp., *Cibotium* 9 sp., *Thyrsopteris* 1 sp., *Cyathea* 182 sp., *Hemitelia* 59 sp., *Alsophila* 185 sp.

C. Sori dorsal or on forking of nerves. Indusium spherical to scaly, or wanting. Annulus mostly homologous. . . . . . (III) CYATHEEAE
  a. Indusium complete, spherical. . . . . . . (5) *Cyathea* (100 sp.)
  b. Indusium incomplete, scaly. . . . . (6) *Hemitelia* (40 sp.)
  c. Indusium wanting. . . . . (7) *Alsophila* (125 sp.)

The Dicksonieae include the larger and smaller tree-ferns with radial structure. The leaves are repeatedly pinnate with marginal sori. The Thyrsopterideae, represented by a single species (*Thyrsopteris elegans*), have compound pinnate leaves and the erect stem, about three to five feet in height, covered with the leaf-scars. The fertile pinnae terminate in sori with cup-like basal indusia. The Cyatheeae, typical dendroid ferns, include about 90% of all species of Cyatheaceae. A few are creeping forms, but most are tree-like. The erect columnar stem is covered closely with leaf-scars. Leaves may be simple or singly pinnate, but usually are compound pinnate, and bear superficial sori.

The anatomy of the Cyatheaceae has been investigated by several authors, whose results are briefly stated here in chronological order.

LINK (1826) described the general structure of Brazilian tree-ferns. The stems are covered densely with remains of leaf-bases. In the stem there is a ring of wood enclosed by brown tissue consisting of prosenchyma. This ring is not continuous, but separated into several segments.

The work of VON MOHL (1833) (German translation, 1845) is one of the important works on the anatomy of tree-ferns, and describes the internal and external structure of some species of *Alsophila* and *Cyathea*. The foliar arrangement is spiral or in rings. The external protective sheath consists of two kinds of tissue, that is, the external parenchymatous and the internal fibrous. Vascular bundles are in several separate segments of V- or W-shape. From both margins of each foliar gap numerous bundles are separated and arranged in a peculiar manner in the petiole; also in the central part of the petiole there are a few bundles, which are the direct continuation of the small bundles distributed in the pith of the stem.

KARSTEN (1849), in his treatise on the structure of palms, described the structure of some ferns. The stem of *Alsophila pruinata* has a ring of vascular bundles, the gaps in which do not overlap. From a gap, a horseshoe-shaped bundle is separated and enters the petiole.

METTENIUS (1856), in his systematic work on ferns, described the structure of ferns, especially of the vascular bundles in the petioles. In the petiole of *Dicksonia*, *Cibotium* and *Balantium*, a single horseshoe-

shaped bundle with incurved margins is present, while in *Alsophila, Hemitelia* and *Cyathea,* numerous separate bundles are arranged in two peculiar arcs, except that *Alsophila armata* has three connected bands and *Alsophila pruinata* a horseshoe-shaped bundle.

METTENIUS (1864) gave, in his work on the anatomy of *Angiopteris* and other ferns, a brief account of the anatomy of the Cyatheaceae. In the stem of *Dicksonia* and *Cibotium,* several curved vascular bundles are arranged in a ring, the margins of each bundle turning outwards. In *Alsophila, Hemitelia* and *Cyathea,* in the inside of such a vascular ring numerous small strands are found, except in some *Alsophila* (*Al. pruinata, blechnoides*). They anastomose into one another in the pith. Surrounding each bundle in the stem is the brown sclerenchymatous sheath. The small bundles in the pith sometimes have such a sheath. In the petiole, numerous strands are arranged in two peculiar arcs.

RUSSOW (1872) described the structure of most families of ferns, but the Cyatheaceae were dealt with in but few words. The general structure of this family is like that of the Polypodiaceae. In the cortex, gum-cells, gum-canals and tannin-canals are found.

SCOTT's work (1874) on the structure of tree-ferns from Sikkim in India (6 *Alsophila,* 1 *Hemitelia,* 1 *Cyathea*) is one of the most important works on the subject. The ring of vascular bundles in the stem is interrupted by several lacunae, from both margins of which numerous leaf-traces are separated. The number of the lacunae is variable not only in the different species but also in the different levels of the stem in one and the same individual. Most of the species contain the medullary bundles, indefinite in number. These bundles appear near a foliar gap, and develop upwards to the petiole and downwards to the pith, in which they end blindly. In the petiole, numerous vascular strands are arranged in a peculiar manner. Older leaves fall off at the basal part of the petioles, or the diaphragm. The smaller grooves at the base of petioles are filled with brown cells. Adventitious buds are often borne on the stem, in some cases extending all around it.

DE BARY (1877), in his "Comparative Anatomy", summarized the earlier works, especially those of METTENIUS, and added his own observations. In the Cyatheaceae, the vascular bundles of the stem are arranged in a ring interrupted in several parts corresponding to the leaf-gaps. The number of the gaps is variable, and when they are numerous each bundle curves in a horseshoe-form. Each bundle is enclosed in a brown sclerenchymatous sheath. In most of the *Alsophila* and *Cyathea*

there are accessory internal strands in the pith. A few pairs of them enter each petiole upwards, while downwards they anastomose into one another and finally end blindly in the pith. In a few species (e. g. *Cyathea Imrayana*) there are also accessory cortical strands, the course of which is not well known. In the petiole, numerous vascular strands are arranged in a peculiar manner, in two curved series; also in the upper part are a few isolated bundles which are the direct continuation of the medullary bundles just mentioned.

THOMAE (1886) dealt with the comparative anatomy of the petioles of ferns, especially of the vascular system. He also remarked briefly on the Cyatheaceae. He divides the vascular system of the fern-petioles into four types, that is, (1) Asplenian type, with one or two bundles arranged in an arc, (2) Aspidian type, with more than two bundles arranged also in an arc, the upper two being called 'superior strands' and the others 'inferior strands', (3) Polypodian type, with numerous bundles arranged in a more complex manner, (4) Cyatheacean type, with numerous bundles arranged in two series, superior and inferior, each in a semilunar form, (5) Marattiacean type, with numerous bundles arranged in a polycyclic manner. Among the Cyatheaceae, in *Alsophila*, *Cyathea* and *Hemitelia* the separate bundles in each series are gradually fused upwards, until they form two bands which are combined finally to form a single strand at the very end of the rachis, while in *Cibotium* and *Dicksonia* the petiolar bundles are not separated but are fused in a U-shape. The branching of the vascular bundles to supply the pinna-axes arises from two lateral corners of each series of bundles, or from the lateral sides of the U-shaped bundles. In the base of the petioles of Marattiaceae and Cyatheaceae there are lenticel-like structures, filled loosely with separate cells. In the former family the phellogen is developed in this structure, while in the latter it is not formed. In the fundamental tissue there are numerous tannin-canals and gum-canals, the former being also included in the bundle itself.

POIRAULT (1893) undertook the anatomical investigation of the vegetative organs of ferns, and devoted a few words to the Cyatheaceae. He states that in the petiole there are large sieve-tubes, on the wall of which numerous crowded sieve-plates are present. In the leaves numerous crystaloids and crystals of calcium oxalate are found.

HANNIG (1898) described the structure, the development and the function of whitish or brownish fusiform tissues, found in the basal parts of the petioles of the Marattiaceae and Cyatheaceae. He classified these tissues according to their positions into two kinds (petiolar

and trunk), though there seems to be no pronounced difference in their structure. They are embedded in the fundamental tissue, and consist of loosely arranged parenchyma. They may have a function as lenticels, but differ in structure from those of Phanerogams. There is no cork-cambium in this tissue of the Cyatheaceae. These are formed under the stomata. On the external surface of the parenchymatous cells there are many minute rod-like processes.

Parmentier (1899) investigated the anatomy of the petioles of ferns, and found that the result could be applied to some extent to the classification of ferns, especially with regard to the vascular system. Among the Cyatheaceae, the pinna-axes (the petioles were not investigated) of Dicksonieae were found to have the single strand peculiarly curved, while those of Cyatheeae had three or four bands with a characteristic arrangement. The latter form may be derived from the former by horizontal as well as vertical division.

Gwynne-Vaughan (1901) described briefly the stelar anatomy of some species of *Dicksonia* with the solenostelic construction. But, the species described do not belong to the true *Dicksonia* but to *Dennstaedtia* of the Polypodiaceae.

Diels (1902), in his systematic work on the Cyatheaceae, described their vegetative organs and anatomical characters. The vascular system in Dicksonieae he found to be constructed on the same principle as the Polypodiaceae, but as they are larger in size, the vascular system consists of thick bands and is accompanied by brown sclerenchymatous bands. Cyatheeae are more complicated by the presence of accessory medullary and cortical strands which have never been found in other ferns.

Gwynne-Vaughan (1901–03) described the stelar anatomy of ferns, especially that of the Polypodiaceae having the solenostelic and related types. The medullary bundles found in many ferns are produced by the internal projection of the solenostele. He makes some observations on the Cyatheaceae. Some species of *Dicksonia* with the solenostele are described, but they properly belong in *Dennstaedtia*. A Cyatheacean *Dicksonia* (*D. Barometz*) has a radial dictyostele, and from the gaps the foliar bundles are parted in an arc-form or in numerous separated strands, which on entering the petiole are arranged in a peculiar manner. The stem of *Cyathea* is of a dictyostelic type with internal strands, a part of which fuses into the base of the leaf-traces, and the petiolar bundles are arranged also in a characteristic manner. He observed also the stele in the young plants of *Alsophila excelsa*. The basal part of this young stem is protostelic. Tracing it upwards, in

the center of the xylem a parenchymatous pith appears, and then the phloem and endodermis are developed, thus forming a solenostele, which soon becomes a dictyostele by the overlapping of leaf-gaps. At the same time, internal strands are produced by internal projection and separation from the stele. In the phloem of the petiole in some species mucilage-ducts are found.

Chandler (1905) described the vascular anatomy of the young plants of a *Dicksonia* and some Polypodiaceae. In these plants, the basal part of the stem is protostelic. Tracing it upwards, a mass of parenchyma is found in the center of the xylem. Then the phloem appears in the center of the latter, and further upwards the endodermis appears due to pocketing from the upper leaf-gap, resulting in the formation of a solenostele. A little further upwards, the latter is broken up into a dictyostelic form by the overlapping of the leaf-gaps.

Schütze (1906) investigated the physiological anatomy of some tropical tree-ferns and a few other ferns. As to the dermal system, he states that there is the subepidermal sheath, the outer part of which consists of parenchyma, and the inner of sclerenchyma. Neither layers is the result of the activity of cork-cambium. The main conducting system of the stem is a peripheral ring of vascular bundles, which is interrupted by several gaps. From the margins of these gaps numerous foliar traces are parted. In some species of *Alsophila* and *Cyathea* there are medullary and cortical bundles. Two or three pairs of the former penetrating the gap enter the petiole, where these strands are situated in the upper median portion. When traversing the gap they either touch or do not touch the stele. It is often found that some medullary bundles having no relation to the gap are united with the stelar surface. The medullary bundles themselves anastomose with each other in the pith. Cortical strands, which are few in number, are united to the outer part of the vascular ring near the gap. In *Dicksonia* and *Cibotium* neither kind of accessory strands is present. The physiological function of these strands may be to transport the assimilated material to the pith or the cortex for reservation, and their connection with the vascular ring may mean the retransporting of the reserved material to the ring. The wood consists of large tracheids, the protoxylem (protohadrom) being situated in the marginal part of each segment of the stem-stele and in the inner central part of the petiolar bundle. The roots are of the normal diarch to tetrarch types. A medullary bundle is circular in a cross section, and the protoxylem is situated in its central part. In the stem and petiole, the phloem

completely encloses the xylem, and outside the sieve-tubes there are layers of 'false sieve-tubes', or tubular elements with pointed ends and pitted walls, containing some albuminous substances. The protophloem (protoleptom) is situated outside the sieve-tubes, and is enclosed by an endodermal layer, the tangential walls of which are not suberized, so that the communication between the bundle and the surrounding tissue is maintained. The mechanical system consists of a stereom-sheath surrounding each bundle. Outside the medullary strands, a similar sheath is present though it is not a thick one, but in some bundles these stereoms are lacking. In the petioles, surrounding each bundle and in contact with its endodormis, there is a fibrous sheath. In the roots, a thick mechanical tissue is present in the cortex. In the fundamental tissue of the leaf and the stem, excretory cells and tannin-canals are present, the former being found also in the phloem of the stem.

SCHOUTE (1906[1]) described the case of the forking of the aerial stem in *Hemitelia latebrosa* and *H. Junghuniana*. He (1906[2]) also found a curious feature in the branching of the stem of *Hemitelia crenulata*.

STEPHENSON (1907) described the structure of the sporelings in three species of *Cyathea* and one species of *Dicksonia*. They are constructed after a similar type. The basal part of the stem is protostelic, while a little above, a central pith appears, and then a solenostele is formed. There are, however, some differences and irregularities. A medullary bundle is formed by the activity of the meristematic tissue in the pith. The petiolar bundle, parted from the basal part of the stem, is arc-shaped, and collateral in structure.

TANSLEY (1907–08), in his well known lectures on the stelar system of ferns, described the evolution of the steles, and dealt cursorily with the Cyatheaceae. The simplest form in this family is found in *Dicksonia Barometz*, which shows a radial dictyostele. In *Cyathea* and *Alsophila*, in addition to such a stele there are internal strands in the pith, which pass down through the pith until they end blindly, while above they enter the petiole. It is uncertain whether these strands are a newly acquired character or a degenerate form of internal strands in the polycyclic stele. In some species, accessory cortical strands are present, the origin and character of which are also uncertain. The arrangement of the petiolar bundles is peculiar. In the branching of the pinnae from the rachis, the vascular bundles of the former part independently from both series of the bundles of the latter, but in this case, there is a short connective strand which connects them.

It is well known that, in the petiole of ferns, there is a cavity opposed to the protoxylem, which is filled with large parenchymatous cells. Mc Nicol (1908) showed that such structures are widely distributed in the ferns, and in the Cyatheaceae they are also well developed, some of them showing a lignified reaction or netted thickenings of the walls.

In his " Land Flora ", Bower (1908) recorded observations on the soral construction and anatomy of all families of ferns and mosses, and discussed the phylogenetic relations between them. On the Cyatheaceae he referred in ditail to earlier observations. *Dicksonia Barometz* and other species of Dicksonieae have stems with the solenostelic or dictyostelic structure, and the petioles with a single bundle. Among Cyatheeae, *Alsophila pruinata* and *Al. blechnoides* have the solenostelic stem and the petioles with a single bundle, but in most of this tribe the vascular system is of a dictyostelic type with accessory strands in the pith and in some cases also in the cortex. The leaf-traces, composed of numerous strands, are disposed in a horseshoe-form with accessory strands among them. In origin and nature, the medullary strands would be comparable to the accessory rods seen in *Dennstaedtia*, while the cortical ones have no correlatives in other ferns. As to the structure of the young plant, Bower referred to the observations by Gwynne-Vaughan.

Pelourde (1909) divided the ferns into four principal types, based on the different forms of the vascular system in the petioles, viz. (1) two bundles with hippocampus-shaped xylem and modifications, (2) numerous bundles arranged in an arc, (3) an arc-shaped bundle with the opening upwards, and (4) the same with the opening downwards. Though the petiolar bundles of the Cyatheaceae are not so simple they may be included in the first type.

Schlumberger (1911) described the different characters of the reproductive and vegetative organs between the Cyatheaceae and Polypodiaceae. The vascular system of the stem shows no absolute difference between them, while the mucilage-ducts are characteristic in the former family. These ducts develop by the fusion of mucilage-cells.

Sinnot (1911) investigated the evolutionary tendency of the leaf-traces, and divided them, according to the structure of their primitive basal parts, into three main types, viz. (1) a single bundle with monarch protoxylem and modifications, (2) two bundles each with a single protoxylem and modifications, (3) a single strand of triangular shape with a protoxylem in each angle and modifications. The primitive type of the last form becomes a flattened arc as in Dicksonieae,

which are divided into numerous bundles in Cyatheeae.

BOWER (1912) described the anatomy and sporangial structure of *Lophosoria pruinata* (*Alsophila quadripinnata*) and concluded that it might be an intermediate type between the true Cyatheaceae and Gleicheniaceae. The stem of this plant is solenostelic, the leaf-gaps scarcely overlapping. Inside the solenostele of the stem, a brown sclerenchymatous sheath is present. A leaf-trace parts from the solenostele as a curved band with lateral constriction, which continues to the rachis as it stands, while in some cases the parted trace is divided into three bands, which are soon united again into one band. An adventitious bud, sprung from the petiolar base, is also solenostelic.

From the anatomy and soral structure, the same author (1913) discussed the phylogeny of *Metaxyla rostrata* (*Alsophila blechnoides*) and the related ferns. *Metaxyla* has a solenostelic stem, and the sclerenchymatous sheath on the stele is not continuous. A leaf-trace is of a continuous peculiar arc-shape. On the basal part of the petiole an adventitious bud is formed which possesses also the solenostelic form. *Dicksonia Barometz* also bears an adventitious runner with a solenostele. On the basal part of the petiole of *Hemitelia setosa*, with a typical Cyatheacean stele, there is also an adventitious bud, of which the larger one has a dictyostele with internal strands similar to those of the stem, while the smaller one has a solenostele with a few strands in the pith. The adventitious runner of *Cyathea mexicana* has a solenostele. The stelar construction of *Thyrsopteris elegans* differs from other Cyatheacean plants in having the stem with a polycyclic stele. The outer ring is solenostelic, and the second is of the irregular dictyostele, one part of which proceeds outwards and closes the outer solenostelic gap formed by the parting of the leaf-trace. The third or innermost ring is composed of a few small strands arranged irregularly. A petiolar bundle is of an irregular arc-shape in the smaller petiole, while in the larger one it is divided into three bands arranged in a peculiar manner.

DAVIE (1918) described the mode of branching of pinna-traces from the rachis-bundles in ferns. There are two main types ; in one of them, the branching occurs from the extreme ends of the rachis-strands (marginal type), while in the other it arises from the lateral sides of the vascular arc (extra-marginal type). The Cyatheaceae, except *Balantium*, present good examples of the second type.

BOWER (1921) pointed out the close correlation of the external features of plant bodies and their stelar system, the evidence of which

was based on his study of ferns. In the ontogenetic development of ferns, the primitive protostele becomes a medullated form and then passes into a solenostele, which is transformed into a dictyostele. In some species of the Cyatheaceae he described and figured the stelar system of stems and petioles.

Posthumus (1924) discussed the stelar structure of the Osmundaceae, Gleicheniaceae and other fossil ferns from the point of their phylogenetic relations, and referred to almost all of the earlier observations of various authors on the Polypodiaceae and Cyatheaceae.

Williams (1925) made the anatomical investigation of two species of *Dicksonia* (*D. antarctica* and *squarrosa*). The stelar system of the stem is a dictyostele provided with the sclerotic sheath. In the base of the petiole, separate vascular strands are arranged in a heart-shape, but in most part of the leaf, they are connected into a band. Mucilage-ducts which are distributed in the cortex and pith of *D. squarrosa* are built by the fusion of mucilage-cells, but in *D. antarctica* the cells are not communicated. Superficial appendages are only simple hairs and not scaly. He also discussed on the size-factor of the vascular system.

Bower (1926) studied the structure of hairs, characteristic in every group of the ferns. Among the tree-ferns, the Dicksoniaceae (Dicksonieae, Thyrsopterideae, Dennstaedtieae) and Proto-Cyatheaceae (*Metaxyla, Lophosoria*) have only filiform hairs, while the Cyatheaceae (*Alsophila, Hemitelia, Cyathea*) have also scaly hairs.

From these earlier observations by various authors above given, we see that the cross sections of the stem are almost circular, and in the peripheral region of the stem is situated the main vascular system, and also that the sclerenchymatous sheath which encloses this vascular ring serves, together with the peripheral hypodermal layer, as the mechanical supporting tissue of the large trunk and heavy leaves.

The vascular system of the stem is constructed in five principal and different types: viz. (1) the simplest type, i. e. the typical solenostele, leaf-gaps almost non-overlapping—*Alsophila pruinata, Al. blechnoides*; (2) the dictyostelic type, the margins of each meristele turning outwards—*Dicksonia, Cibotium,* some species of *Alsophila* (*Al. comosa, australis, Maccarthurii*); (3) the dictyostelic type with medullary strands—*Alsophila, Cyathea, Hemitelia*; (4) the dictyostelic type with medullary and cortical strands—some species of *Alsophila* (*Al. crinata, eriocarpa, aculeata, caracassana*) and *Cyathea* (*C. Imrayana, usambarensis*); (5) the

polycyclic stele, one part of the inner circle enclosing a gap of the outer ring—*Thyrsopteris.* Thus, the typical form of the vascular system of the Cyatheaceae is dictyostelic, the meristelic margins of which curve outwards, each meristele being enclosed by a brown sclerenchymatous sheath. This type of structure is found in Dicksonieae, while the typical dendroid Cyatheeae, including about 90% of the whole species of the Cyatheaceae, are characterized by the presence of accessory bundles in the pith, and in some cases also in the cortex. Medullary strands anastomose into each other in the pith, but with regard to their terminations the statements of various authors do not agree. Above, they ascend through the pith, and (1) passing through the leaf-gap enter the petiole, and become some of the petiolar bundles, or (2) in the same course they undergo a partial attachment to the stelar margin, or (3) they fuse into the stele with no direct connection with the leaf-traces. Downwards, they descend through the pith until they either (1) end blindly in it, or (2) fuse into the main bundle. As to the course of the cortical strands, it may be assumed that they fuse upwards with leaf-traces and end blindly downwards in the cortex, though this point has not been decided by actual observations. It may be of interest to note here that *Alsophila blechnoides* and *Al. pruinata,* which have solenostelic stems, are classified by some authors in other genera, and that *Thyrsopteris elegans,* which has a polycyclic stele, is considered to be a monotypic genus.

The number and arrangement of the vascular strands in the petiole varies according to its different levels. When the basal parts are compared, (1) the simplest type possess a single arc-shaped bundle with incurved margins and constricted sides—*Alsophila pruinata, Al. blechnoides*; (2) a similar arrangement divided on the lateral sides into three segments—*Thyrsopteris, Dicksonia, Cibotium*; (3) numerous bundles arranged in a circular form with additional strands on the lateral and upper parts projecting inwards—*Alsophila, Hemitelia, Cyathea.* That is to say, in Dicksonieae and Thysopterideae three bands are arranged in an arc, which upwards are fused into a single continuous arc-shape, while in Cyatheeae numerous strands are arranged in a characteristic, more complicated manner, and upwards are fused gradually into simpler bands, but the superior and inferior series do not fuse, to each other, except at the very end of the rachis.

The mode of branching of pinna-traces from the rachis-bundles is of the so-called extra-marginal type, that is, in Cyatheeae, in the rachis of which both series are distinctly separated, the pinna-traces are

separated from the corners of both series respectively, while in Dicksonieae, in which the rachis-bundles are arranged in an arc-shape, the pinna-traces are separated from both sides of the lateral constriction and are arranged also in an arc in the pinna.

Anatomically speaking, the thin brown sheath of the stem surface consists of outer parenchymatous and inner sclerenchymatous layers. The meristele is constructed according to an amphicribral concentric type, enclosed in a distinct endodermal layer. The xylem consists of tracheids and parenchyma, the former being large and scalariform. The phloem consists of sieve-tubes and parenchyma, in the external part of which a distinct layer of crushed protophloem is found. Inside the protophloem are secretory cells. The fundamental tissue consists of parenchyma, in which numerous mucilage-canals and similar secretory cavities are embedded. The sclerenchymatous sheath surrounding each meristele consists of fibers. A detailed study of the structure of the medullary and cortical strands is lacking.

In the petiole, under the epidermis there is a layer of fibrous tissue. The fundamental tissue is parenchymatous, and in it the petiolar bundles are embedded. Each bundle is of an arc-shape with the xylem in the center. The protoxylem occupies the inner central part of the xylem-arc, and a cavity accompanied by tylosis is found in front of the protoxylem. Surrounding the xylem there is a ring of the phloem in which mucilage-canals and fibers are often included. Outside the vascular bundle there is an endodermal layer accompanied by a fibrous sheath outwards. The general structure of band-formed bundles is not essentially different from the separate ones above referred.

In the broad cortex of the root a great amount of mechanical tissue is developed, and in its stele a normal diarch to tetrarch radial bundle is found.

The stem often bears several adventitious buds, on account of which, in some cases, the apparent bifurcated or trifurcated types may be seen. They are also found in the external side of petiolar bases.

Concerning the ontogeny, the root in the sporeling has a diarch stele which is continuous to the protostele of the stem. Tracing the latter upwards, in the center of the xylem there appears a parenchymatous pith and then the phloem, and a typical solenostele is formed by the pocketing of the endodermis. A dictyostele results from the solenostele by the overlapping of leaf-gaps. The medullary bundles begin to appear at some distance from the basal part of the stem by internal thickening of the main bundles or by independent formation in the pith.

From the historical sketch above given we see that there are some discordant points in the results of the observations. For example, on the origin of the medullary bundle, one author insists that it appears in the pith independently, while another maintains that it is formed by the internal projection of the stelar ring. Also, on its upper termination there are differences of opinion. Thus, we see that our knowledge of the structure of the Cyatheaceae is neither complete nor certain, probably because of the difficulty of procuring the material, as they inhabit tropical regions, and are also too large to be transported as fresh or alcohol material.

For several years past, the writer has been working on the anatomy of ferns, and lately commenced a comparative anatomy of the Cyatheaceae, the results of which will be published in this paper. The material has been collected in various parts of Japan. The research has been carried on in the Botanical Institute, Faculty of Science, Imperial University of Tokyo.

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II. Cyathea spinulosa, Wall.*

Cyathea spinulosa is one of the tree-ferns distributed widely in Japan, Southern China, Malacca and North India. In Japan, it is found in the Bonins, Loochoo and Formosa, but it occurs also in Hachijô, a small island situated in latitude 33° 5′ N. and longitude 139° 50′ E., or 170 knots south of Tokyo, which is perhaps the northern limit of the habitat of tree-ferns. The materials examined were collected on this island in April, 1924.

I. The Adult Plant

The stem of *Cyathea spinulosa* is erect and covered by the remains of petiolar bases. Petiolar bases are very rigid and remain for a long time after the fall of the leaves, covering the stem surface almost permanently. Adventitious roots are given off abundantly all around the stem, and together with the petiolar bases serve as the protective sheath of the stem. The petiole is pretty long, and the compound lamina expands broadly. The leaves, however, are limited to the upper part of the stem. The older leaves fall off leaving their hard bases, thus giving the fern the general aspect of a palm or cycad. The roots on the basal part of the stem lengthen and branch out repeatedly, densely covering the stem and petiolar bases. These roots are much entangled, and it is almost impossible to trace any one of them, but some of them reach the ground and may serve as absorptive organs, while others may serve as absorptive though they do not reach the ground, as is the case with epiphytic plants. As a matter of fact, the root-mass at the stem base is used as a stand in the culture of orchids and other epiphytes, for which it is well-suited. The roots borne on the upper part of the stem are always too short to reach the ground, and most of them are dry, so that, they may be of no use as absorptive organs.

The height of the stem varies according to age and habitat. There is no exact record of the maximum height. On Hachijô the writer found a plant that was more than 6 meters in height, while in the Bonin Islands they grow even to a height of 10 meters. The leaves on the

* The contents of the Part II appeared in Japanese in the Botanical Magazine, Tokyo, Vol. 39, pp. 1–28, Jan. 1925.

upper stem are stouter and larger than those on the lower, sometimes reaching more than 3 meters in length. The thickness of the stem itself cannot be measured exactly without removing the coverings of the leaf-bases. In one collected by the writer, it was about 15 cm. in diameter.

The stem is usually erect growing straight or slightly inclining, but in rare cases, its basal part may creep along the ground. The stem bears no branches.

The phyllotaxy or the mutual arrangement of the leaves of this plant is not constant, it differs according to age or height of the stem, and a gradual change in the phyllotaxy may be observed in one and the same plant. Such a change in the phyllotaxy is found, as a rule, in tree-ferns. SCOTT (1874) recorded a number of such examples. The writer's own observations show that the phyllotaxy of the lower part is $\frac{2}{5}$, and that of the upper part $\frac{3}{8}$, while in the intermediate region transitional forms are observed. A phyllotaxy higher than $\frac{3}{8}$ may also occur.

A. CROSS SECTION OF THE STEM

Before describing the minute structure of the stem, it will be convenient to begin with the general structure in cross section, which shows a typical Cyatheacean form. It is almost circular in shape with a diameter of 7 cm. in one of the specimens measured. Where the petiole is attached, the periphery of the stem bulges out a little; consequently, its outline becomes irregular (Fig. 1).

The peripheral part is made up of brown tissue about 1–3 mm. thick, which serves as a protective sheath. The fundamental tissue consists of whitish parenchyma, on the peripheral region of which is a stelar ring (Fig. 1, st), protected on both sides by hard brown sclerenchymatous bands (Fig. 1, sc). In the central pith, there are numerous medullary bundles scattered uniformly (Fig. 1, md). Detailed accounts of each part will be given in the following.

a. The Stele

The stele forms a discontinuous ring interrupted in several places which correspond to the leaf-gaps (Fig. 1, st). These gaps are usually five in number, though four or six gaps are occasionally found. These gaps

are not at equal distances from one another, which is due to the fact that the arrangement of the leaves is not $\frac{2}{5}$, but $\frac{3}{8}$ in a right-handed direction. The margin of each meristele curves outwards, and consequently, the shape of a meristele is neither a straight line nor a simple arc. The smaller meristele is almost of a V-shape, while the larger one is like a

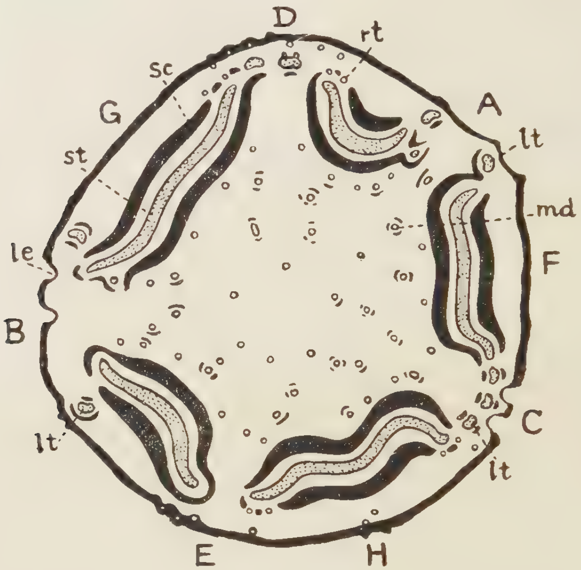

Fig. 1. Transverse section of the stem. (nat. size)

A–H, position of leaf-gaps
st, stele
sc, sclerenchymatous sheath
md, medullary bundle
lt, leaf-trace
rt, root-trace
le, lenticel

flattened U, the main part being straight and both margins curved outwards, or the main part bulges out a little making a wavy or W-shape (Fig. 1). In the latter case, the middle convex part of the W corresponds to the part where the gap at the upper level begins to open or where the gap at the lower level has just been closed (Fig. 1, F–H), that is, it corresponds to the top or bottom of a leaf-gap. From the position of these bulging places and the true gaps (Fig. 1, A–H), it is easy to determine the phyllotaxy being $\frac{3}{8}$, as has been stated. The thickness of individual meristeles is almost uniform, and decreases slightly toward the margin.

b. The Sclerenchymatous Sheath

The sclerenchymatous sheath consists of brown sclerenchymatous fibers and encloses each meristele, from which it is separated by a parenchymatous layer (Fig. 1, sc). The sheath encloses each several meristele forming a complete ring, but on the marginal regions numerous interruptions or pores are seen, which are the spaces where leaf-traces and root-traces penetrate. These interruptions are very numerous, as the leaf- and root-traces are abundant. No pores of the sheath other than formed by these traces have been found.

c. The Leaf-Trace

Leaf-traces, which are numerous in numbers, part mostly in pairs from both margins of the leaf-gap (Fig. 1, lt). In a transverse section of the stem, only a few pairs of them are seen in each gap, though there are, on the whole, more than ten pairs to each gap. This is due to the fact that, the traces once parted from the meristele ascend upwards and outwards through the outer cortex, and the traces which have separated off before (that is, from a lower level) leave the stem surface before the next traces (that is, those of the upper level) part from the meristele (Fig. 1).

Leaf-traces are accompanied on their inner and outer sides by small brown sclerenchymatous bands, which are a continuation of the same tissue found on the meristele.

d. The Root-Trace

The roots, which are always adventitious, cover all sides of the stem, apparently with no system in their arrangement, but, if carefully examined, they are found to part from the stem in connection with leaves, that is, the root-traces part from both margins of leaf-gaps or from the basal parts of leaf-traces (Fig. 1, rt). They are very numerous in each gap, and when they part from the meristele, they penetrate the sclerenchymatous sheath making there small pores, and then they traverse the cortex downwards, and leave the stem surface. The writer has never met with a case of traces parting from the main body of the meristele, that is to say, there are no traces that are not connected with leaf-gaps.

c. The Medullary Bundle

One of the characteristic features of the Cyatheacean stem is the presence of the medullary bundles. In the present species, there are numerous medullary bundles scattered in the pith (Fig. 1, md), fourty or fifty of them being found in a transverse section of the stem. The presence of the small ones is liable to be overlooked, while the larger ones are very distinct, as they are accompanied by the brown sclerenchymatous masses. The position of these masses in each bundle is not constant. In general, the larger bundles are accompanied by the larger masses of sclerenchyma, and in some of the smaller bundles they may be lacking. Their number is also indefinite, but usually one to four segments are arranged in an interrupted ring.

Sometimes, two bundles fuse into each other in an elliptical form in a cross section, or one bundle bifurcates in the pith, thus showing the fusion and branching of medullary bundles.

Though the medullary bundles are not distributed in a regular manner, they have a tendency to be more numerous in the periphery of the pith. At the margins of the meristele, they traverse its sclerenchymatous sheath, and acrossing the parenchymatous layer unite with the meristele. The sclerenchymatous masses on the medullary bundles also fuse into the same tissue of the meristele. The medullary bundles which are about to fuse with the meristele are always in pairs. We have never met with a case in which they unite with the middle part of a meristele.

Cortical bundles which are found in some species of the Cyatheaceae are not found in this plant.

B. Solid Construction of the Stem

For the complete understanding of the size and mutual relation of the leaf-traces and root-traces, the course of the medullary bundles, etc., a large number of sections must be compared. As, however, the stem of this plant is massive and is accompanied by hard sclerenchymatous sheaths, it is difficult to get successive transverse sections of the entire stem. The writer made a large number of partial sections of the stem, by the combination of which the solid construction of the stem, especially of the stele, has been studied. Thus, he got a stelar construction of a stem with a diameter of 7 cm. (Fig. 2). Its structure will be described below. In the following description, the tracing of the tissue was done from below upwards.

a. The Stele

The stelar system of this trunk has the form of a tubular cylinder with long leaf-gaps in its wall (Fig. 2). The marginal portion of each gap curves outwards. The gap of the cylinder has a very long fusiform shape, 10–15 cm. in length and 1.0–1.5 cm. in breadth. The maximum breadth of the gap is not at the middle part of a gap, but lies much nearer the top. Moreover, the margin turns outwards, but the outline of the margin is not simple-fusiform, as it has a constriction on each side on the upper part of the gap, where the gap attains its maximum breadth (see also Fig. 5).

Fig. 2. Reconstruction of the stelar system of the stem. (nat. size)

From both margins of a gap numerous leaf-traces part successively. Mutual gaps overlap one another, and by their position it is easy to determine the phyllotaxy, which is right-handed $\frac{3}{8}$. Thus, the stele is considered to be of a dictyostelic type.

b. The Sclerenchymatous Sheath

As the sclerenchymatous sheath is an envelop closely accompanying with the stelar system, its position and shape coincide almost exactly with the outline of the stele. Where there is a stelar gap, there is also a gap on the sheath. Tracing upwards from the level where a gap is about to open, the inner and outer bands of the sheath approach, and unite with one another forming an X-shape in cross section, the right and left halves of which soon separate at the middle part, and then enclose both margins of the meristeles (see Fig. 4, 1–3). When a gap is about to close, this process is nearly reversed (Fig. 4, 18–21).

Fig. 3. A part of the sclerenchymatous sheath of the stem on cutting off the outer cortex to show the arrangement of leaf-traces and root-traces penetrating the sheath. Root-traces are shown as dark holes at the basal part of the leaf-traces.

(nat. size)

The sclerenchymatous sheath is interrupted at the margin of the gap by small perforations, through which leaf- and root-traces penetrate (Fig. 3).

c. The Leaf–Trace

Previous to describe the solid construction of the leaf-traces, the arrangement of foliar bundles in the petiole must be explained. In the basal part of the petiole, 40–50 bundles are arranged in a peculiar form (Fig. 7, A). Most of them are disposed in an elliptical form, parallel to the surface of the petiole, but in addition to these there are series of several bundles on the lateral and upper parts projecting inward from the elliptical ring. In the lateral series, they are arranged in two rows, the lower of which consists of two or three bundles, while the upper of five or more bundles which project beyond the lower. The projecting bundles at the upper part, two to four in number, are in a group. The upper row of the laterally projecting bundles and those of the upper half of the elliptical ring, including the upper projecting group, may be called the "superior strands", and the lower row of the laterally projecting bundles and the bundles of the lower half of the elliptical ring may be called the "inferior strands". The division of these two groups of strands was proposed

Fig. 4. Successive cross sections through a leaf-gap to show the mode of branching of leaf-traces and root-traces and the course of the medullary bundles. (nat. size)

Explanations in text.

for the first time by THOMAE (1886, Oberstränge und Unterstränge).

The leaf-traces belonging to a petiole separate off from both margins of a leaf-gap at different levels successively, usually in pairs (Fig. 4 & 5). The first pair, the lowest, parts not from the very base of the gap, but from about 3–4 cm. above the latter. The gap is narrow at the basal part, and becomes gradually wider upwards, and at the level where the second pair separates off, 2–3 cm. above the first, the breadth of the gap is about 2–4 cm. (Fig. 5). The third pair parts 1.5–2.0 cm. above the second ; the fourth lies 1.0–1.5 cm. above the third, and so on. Thus,

the interval between two successive partings decreases gradually upwards (Fig. 5). Several pairs of the leaf-traces thus parted enter the petiole, in which they are arranged in an arc in the lower or external part.

The stelar margins at a leaf-gap curve outwards, the tendency of which is not distinct at the base (Fig. 4, 3–6), but gradually becomes more marked upwards (Fig. 4, 7–9), until the margin of the meristele turns out almost 180°; consequently, the parted traces are situated at the outside of the margin, and at the same time at its lateral side (Fig. 4, 10–13). The last pair (7–9 th. pair) thus parted from the margin corresponds to the bundle at the uppermost corner of the inferior petiolar strands. Then, the stelar margin of the gap begins to recover its turning. Just at this point, one or two pairs of traces are separated almost simultanously, which correspond to the laterally projecting bundles of the inferior series (Fig. 4, 11–14). In this way, the gap-margins become narrow, corresponding to the constriction mentioned above.

Fig. 5. Reconstruction of a leaf-gap to show the mode of branching of leaf- and root-traces and the course of the medullary bundles. External view. (nat. size)

Soon, the stelar margin at the gap begins to curve outwards again, and in its course, several traces are parted in the same way as before (Fig. 4, 15–18). The bundles thus detached correspond to the laterally projecting ones of the superior series. The last pair parted from the extreme curved margins corresponds to the petiolar bundles at the corners of the superior series. Next, the gap becomes narrower, but the margin retains its turning tendency, and from the margin successive traces, usually close to one another, separate off, and at last the remaining curved part on each side is separated, in a band-form, from the meristele, the band soon being divided into three or four small bundles (Fig. 4, 18–19). These bundles are those of the upper arc of the superior series. The last pair thus divided is situated in the middle of the upper arc, and the two strands from both sides of the gap approach, and are arranged in a continuous upper arc. The leaf-gap then becomes very narrow, and at a short distance above the parting of the last pair, it is completely closed (Fig. 4, 20–21).

Two or three leaf-traces often part from the meristele as a common strand, which is divided in its course through the cortex or in the petiole. Such is often the case with the parting of the superior strands, and always the case with that of the last pair.

d. The Medullary Bundle

It is very difficult to trace the course of every medullary bundle. The entire course of a medullary bundle is so long that it cannot be traced, but it seems to be more than 30 cm. reckoning from the case of the young material. An account of the complete course, therefore, will be given in the case of the young material.

Though the medullary bundles are not arranged regularly, two or three pairs near the gap are arranged in two radial rows, and are somewhat larger than the others. If we trace them from the base upwards (Fig. 4), these pairs gradually approach the opening of the gap, and penetrating the sclerenchymatous sheath unite with the bulging parts of the curved meristelic margins (Fig. 4, 9–11). The parts of the meristele, with which the medullary bundles unite, soon part from the meristele, and become the leaf-traces. The union of the medullary bundles takes place in a definite manner. When the margin of the meristele recovers its outward curving and the last pair of the inferior series is about to separate, the first pair of the medullary strands unites with the inner surface of the meristele (Fig. 4, 10–11), and forms a protuberance for a short distance. Meanwhile, the anterior margin of the meristele beyond the point of the protuberance begins to part off, and becomes the last inferior strand (Fig. 4, 11–13). Thus, the point of union of the medullary bundle and the stele becomes the margin of the remaining meristele (Fig. 4, 11–12). Then, this marginal part including the protuberance is separated off, and becomes the first bundle of the superior series (Fig. 4, 13). In a word, the first pair of the medullary bundles unites with the first pair of the petiolar traces belonging to the superior series, which projects deeply into the lateral part of the petiolar bundles.

The union of the second pair of the medullary bundles to the meristele takes place precisely in the same way, and the bundle thus united becomes a leaf-trace belonging to one of the superior series (Fig.4, 11–14). In a gap, three or four pairs of medullary bundles unite with the stele successively. In the case of four, the third pair does the same to the second. The last pair combines with the last pair of leaf-traces. In this

case, the mode of union differs somewhat from that of the preceding pairs. When the gap becomes narrower, successive leaf-traces belonging to the upper arc of the superior series separate off, though the margin retains its tendency to curve outwards. The last pair of medullary bundles approaches the narrowed gap, and unites with the inner bulging surface of the curved part at the opening of the gap, the result of which is to give the margin of the stele a forked appearance (Fig. 4, 15–18). Now, this forked end parts from the meristele, as a whole, in a short plate-form. The latter is then divided into three or four, and becomes the leaf-traces situated in the median part of the upper arc of the superior strands (Fig. 4, 18–20). The innermost of these divided strands, that is the last trace, is derived from the part of union of the medullary bundle and the stele. Thus, the last pair of the medullary bundles may be said to unite with the last pair of leaf-traces of the superior series at the upper median part.

When the last pair of the medullary bundles approaches the meristele and is about to unite with it, the bundle bifurcates (Fig. 4, 16). It is the inner branch of the two which joins the meristele in the way just mentioned. The outer branch separates from the inner, and soon leaves the stem (Fig. 4, 16–18). This is a pair of leaf-traces projecting from the upper arc, that is, of the upper projecting bundles. These traces, therefore, are the peculiar ones in direct continuation of the medullary bundles, and with no direct connection with the meristele itself. There are from two to four such traces. In the case of two, they are derived in the way just stated, while when they are more than two, the upper two are formed in a similar way, and the others are derived from the branches of other medullary bundles in the same way as the ones above.

Therefore, the medullary bundles related to a leaf-gap unite with the bases of the leaf-traces belonging to the superior series, that is, the first pair of the medullary bundles to the first pair of the traces, the last to the last, and the intermediate ones, if present, to some of the superior series, while the branches of some bundles go on directly to the upper projecting strands. Medullary bundles which unite with the meristele other than the leaf-traces or any other parts are not found in this plant.

Thus, we have seen the fate of the upper ends of the medullary bundles. Now, if we trace them downwards, three or four pairs belonging to a leaf-gap unite with each other and become a single pair, which descends through the pith vertically for a long distance, and finally

ends blindly in no connection with the stele. The total length of a medullary bundle is very long, and as stated before, cannot be traced completely. Moreover, the medullary bundles do not always pursue a straight course, but fuse or branch repeatedly, forming an anastomosing network, which makes the tracing of the bundles more difficult. Therefore, the course of the medullary bundles in the adult plant is only to be inferred from the case of the young plant, which will be fully described below.

C. Structure of the Leaf

The leaves are tripinnate and borne on the top of the stem. When they die off, they leave the brown basal parts of the petioles, which permanently cover the stem surface, and serve, together with the root-system, as the protective sheath. The leaves are very large reaching more than 3 meters in length. The proportion of the petiole to the lamina varies considerably, that is, in one case the petiole occupies half of the leaf, while in another case it is short occupying only one-fifth. The largest pinna is not the basal one, but is situated some distance above it. In the petiole as well as in the rachis, a thick superficial mechanical layer persists for many years, while the inner soft tissue decays and is left out. The petiolar bundles also persist for a long time. On the surface of the petiole and rachis, especially on the lower side, there are many hard brown spines, from which the specific name "*spinulosa*" is derived. Along the lateral sides of the petiole and rachis, lenticels are arranged in a straight line, separated at some distance from one another. Spines and lenticels on the basal part of the petiole are larger than those on the rachis. The young coiled leaves are closely covered with brown hairs and scales, while the expanded foliage is almost destitute of them.

a. The Petiole

The structure of the petiole, especially that of the vascular system, varies in its different parts, and it may be convenient to begin with the description of a transverse section at the basal part.

The transverse section of the basal part of a petiole shows a semi-circular outline, the upper side being flat (Fig. 7, A). The size of the petiole differs considerably according to the size of the leaf. The larger one reaches about 3 cm. in lateral diameter. On the surface there are many spines, and on each lateral side there is a small groove corresponding to a lenticel. The surface is protected by a mechanical tissue, in which white fundamental tissue is enclosed. Embedded in the latter

many small vascular strands are arranged in a peculiar manner as before described.

Each of the petiolar bundles presents a small V-shape, those belonging to the inferior series being somewhat larger and more separated from one another than those of the superior series. Each bundle points a definite direction, that is, the opening of every V faces the center of each of the two curves formed by connecting the bundles of the superior and inferior series respectively, so that, the bundles of the lower arc of the inferior series open upwards, while those of the upper arc (laterally projecting bundles) of the same series open downwards. Occasionally, two neighbouring bundles approach or unite. The definite arrangement and orientation of these bundles is an important feature in the anatomy of the petiole, and has a direct relation to the curving of the margins of the meristeles.

In a transverse section of the stem, on the inner side of the meristele at a short distance from the margin, there is a small groove in the xylem, and at a short distance from this groove toward the center of the meristele, the marginal part is cut off, the detached portion becoming a leaf-trace. The xylem of the leaf-trace thus parted off is bent in a V-shape, the opening of which corresponds to the small groove just described. The other tissue of the leaf-trace follows the shape of the xylem, so that the leaf-trace itself is of a V-shape. As the groove of the meristele occurs always on the inner side of the latter, the opening of the V must face the inner side of the stem, or the upper side of the petiole. But, as the margin of the meristele turns outwards in definite places, the openings of the traces parted from such places must face the external side of the stem, or the lower side of the petiole. This accounts for the occurrence of the inversely oriented leaf-traces. From the intermediate regions, the traces with intermediate orientations are separated off, so that a circular series with a definite orientation is formed. As the curving process of the meristelic margins occurs twice, leaf-traces are arranged in two series of rings.

The outline of a petiole in the basal part is semicircular with a flattened upper side, but in tracing it toward the tip, it becomes circular and smaller in size. The upper surface of the petiole is green in colour, while the lower surface is dark brown. Spines which are prominent in the lower basal part reach 4 mm. in length. Lenticels which are arranged on both sides of the petiole are of a long spindle-shape and of variable size, but in general, those of the basal part are larger being 8–10 mm. in length, and 1–2 mm. in breadth. Lenticels in the basal part

of the petiole become hollow on losing their contents (Fig. 6).

The basal part of the petiole is almost parallel to the stem. Therefore, the surface of its attachment makes an elongated ellipse with the vertical axis measuring even 15 cm. and the transverse axis only 1.5 cm. (see also Fig. 3). The transition of the petiolar base into the stem surface is so gradual that the line of demarcation is not clear. In the basal part, lenticels are dislocated toward the outer side, and in the transitional region they are situated side by side on the median line of the outer surface of the petiolar base, and finally they entirely disappear (Fig. 6). In the basal part, a few scaly hairs are left, while most of them fall off. These scales are borne on small processes on the surface of the petiole.

Fig. 6. Stem surface showing the basal parts of three petioles, roots and lenticels. (nat. size)

The petiolar bundles in the basal part are rather numerous; there being about fifteen in an adult form. These bundles are separated and are arranged in two series as before mentioned (Fig. 7, A). It is often noticed that two neighbouring bundles are in a state of fusion. Tracing the petiole upwards, each of the V-shaped opening of bundles becomes wider, and neighbouring bundles approach each other. Further upwards, this tendency becomes marked, and at the upper part of the petiole, two or more neighbouring bundles are united, though separate ones are also present. The fused bundles maintain their original form and orientation, so that, when two are fused they form a W, and in the case of more than two, a continuous wavy form is established. The union of bundles takes place between those belonging to each of the two series, but not between those of different series. Meanwhile, the arrangement of the bundles undergoes a gradual change. The upper arc breaks at its median part, and opens to right and left; its incurved margins unite with the upper projecting bundles, forming the half-coiled margins in the median line. At the same time, the laterally projecting bundles, or the lower arms of the superior series, project more toward the center of the petiole (Fig. 7, B).

b. The Rachis

The rachis is a continuous part of the petiole, and on both sides of it the pinnae are borne in regular order. The outline of the basal part of a rachis in cross section is almost circular, but proceeding upwards, it changes gradually, and in the middle part it becomes a rounded rectangular form (Fig. 7, C), and finally, near the end it is elliptical (Fig. 7, D). The mechanical tissue on the surface of the petiole continues up to the end of the rachis. Lenticels on the lateral sides and spines on the surface are also present up to the end, though they become smaller. Brown hairs, which are abundant in the young stage, especially on the superior surface, fall off leaving only a small number.

In the rachis, the gradual change of form and arrangement of the vascular bundles, which has been observed in the petiole, proceeds further. The union of the separate bundles, the tendency to which becomes evident on the upper part of the petiole, is here more prominent, and the neighbouring bundles are assembled into four groups; two superior and two inferior (Fig. 7, C). The place of fusion of the bundles to form wavy groups is not constant; in one case it occurs near the end of the petiole, while in another it is in the middle part of the rachis. Two superior bands, with a Γ7-shape, are situated side by side. The longer arms of both bands, which are the continuation of the laterally projecting bundles, approach each other towards the center, and the shorter arms, which are the continuation of the upper projecting bundles, curve inwards, but are separated by some fundamental tissue. Two inferior bundles, each of a auricle-shape, are derived from the petiolar bundles of the inferior series by the separation of the middle part of the lower arc. Each of these four bands is a continuous wavy one derived from the fusion of the original V-shaped bundles. The number of waves in each band does not agree with that of the corresponding bundles in the petiole, being always less, the reason for which lies in the reduction of the waves by the complete fusion of the neighbouring bundles. This process of reduction of the waves occurs from the base of the rachis up to the end, where the bands

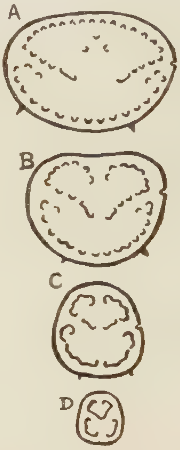

Fig. 7. Transverse sections of four parts of a leaf-axis to show the arrangement of vascular bundles. (nat. size)
A, Base of the petiole
B, Top of the petiole
C, Middle of the rachis
D, Top of the rachis

with few waves are formed.

Meanwhile, the form of the bands undergoes a change. In the first place, the longer arms of the superior bands approach, and finally fuse into one another, thus forming a large V-shaped band with incuved margins. This happens in the distal half of the rachis. In this state, the V-shaped superior band has seven to nine waves, while the inferior ones show only two or three waves respectively (Fig. 7, C–D).

Proceeding further upwards, the lower arms of two lower bands also approach each other, and fuse in the median part forming a flat V-shaped arc. In this way, the superior and inferior series of the petiolar bundles are united respectively in two V-shaped arcs (Fig. 7, D). Still further upwards, each arc flattens more and more, and at the very end of the rachis, the two are united and form a single bundle.

Thus, the union of the petiolar bundles takes place in the superior and inferior series respectively, quite independent of one another, up to the very end of the rachis. The classification of the petiolar bundles into two series, which was proposed by THOMAE, seems to be justified.

c. The Pinna

The base of the pinna-axis, which is borne on both sides of the rachis, varies in size according to the level of the attachment. The base of the pinna-axis attached to the basal part of a rachis has a circular outline with a diameter of about 5 mm., and diminishes in size toward the end of the rachis. With the change in size, the internal structure of the pinna varies, but its principal structure is like that of the rachis. For instance, the basal part of a pinna-axis attached to the basal part of the rachis has a structure similar to that of the upper part of the rachis, that is, surrounded by the hard mechanical layer there are three or four wavy vascular bands. When there are four, two superior and two inferior bands are arranged just in the upper part of the rachis, and when there are three, one superior and two inferior bands are arranged in the same way as in the rachis. Tracing this pinna-axis upwards, the change of structure which occurs in the bundles is also the same as that of the rachis, that is, four bands become three and then two, until at last, a single bundle is formed at the very end. A pinna-axis with a diameter of 2 mm., branching from the middle part of the rachis, has three bands, and that with a diameter of 1 mm., from the upper part of the rachis, has two bands. The mode of fusion of the bundles is similar to that in the rachis though simpler than in the latter.

The mode of branching of the pinna-traces from the rachis-bundles is so characteristic that it may be worth while to describe it here. In essential points, it is almost the same, though it varies a little in detail. When we follow the pinna-traces upwards from the region where it is attached — for the sake of convenience the case of branching to the left side is described (Fig. 8) — the outline of the rachis bulges out slightly to the left, and the rachis-bundles also bulge out in the same direction (Fig. 8, 1–2). The part where this bulging occurs is somewhat above the middle of the lateral sides, corresponding to the corners of the arcs of the superior and inferior bundles. It is at these two corners that this bulging occurs. As the bulging of the rachis proceeds further, the elongation of the bundles becomes more prominent, until at last both arcs will be constricted at some distance from the corners (Fig. 8, 3–4), and two small strands are separated, each in a ring-form, from the constricted parts (Fig. 8, 4–5). The main bundles soon recover their peculiar forms. Meanwhile, these two separated bundles, the pinna-traces, undergo a slight change. In one case, at some distance from the corners of the elongated bundles, on the upper part of the superior series and on the lower part of the inferior series, the continuous arc is broken; the broken parts correspond to the median parts of both separated traces (Fig. 8, 4–5). In another case, the interruption of the traces occurs before they are separated from the rachis-bundles. The upper arc of the separated inferior trace is then broken in its median part, and these two inferior bands form with a V-shaped superior one, which also frequently bifurcates, the typical arrangement (Fig. 8, 5–6). In smaller pinnae, these two separated traces remain undivided.

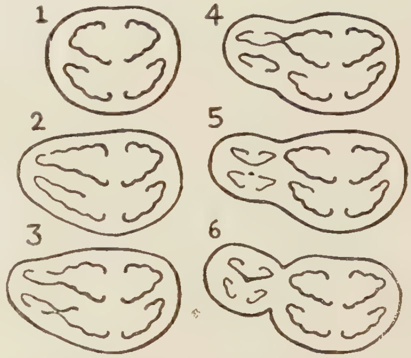

Fig. 8. Successive cross sections at a part of a rachis to show the mode of branching of pinna-traces. (nat. size) Explanations in text.

In the branching of the pinna-traces, it is remarkable that each of the superior and inferior groups of pinna-traces branches off from the corresponding bundles of the rachis. Both series of traces, however, are connected with each other by a small short strand in the branching part. When the upper side of the inferior band of the separated traces is broken in its median part, a small strand is given off from that region (Fig. 8, 5), and runs obliquely up to the lower corner of the V-shaped

superior bundle (Fig. 8, 6). The connection by such a strand is figured by TANSLEY (1907–08) in the case of *Cyathea*. The mode of branching of pinna-traces, therefore, is a typical case of the so-called extra-marginal type of DAVIE (1918).

The branching of the second pinna-traces from the pinna-axis takes place in the same way as in the case of the pinna-traces parted from the rachis-bundles. In the case of branching of the third or last pinna-traces from the second pinna-bundles, the same process takes place.

D. Structure of the Root

The roots, which are adventitious as in many ferns, are given off from the basal regions of the petioles. Their length is inconstant, but rarely reaches 10 cm., while the thickness is pretty constant being 1.0–1.5 mm. But, as the stem is erect, they do not reach the ground, except those of the basal part of the stem. These roots pass out through the crowded petiolar bases.

The parting of root-traces from the stem stele takes place at the base of the petiole, that is, it is related to the branching of the leaf-traces as in many ferns. As a matter of fact, the root-traces are given off from both sides of the lower half of the leaf-gap, or from the bases of the leaf-traces parting (Figs. 2 & 5). The lowest trace belonging to a gap parts from a point a short distance below the bottom of the gap, while the uppermost one parts from the middle of the gap (Fig. 5). On both sides of the gap between these two extremes, numerous root-traces issue successively without any order. Sometimes, two or three traces are given off close to each other. The root-traces thus parted descend downwards, and penetrate through small pores in the sclerenchymatous sheath (Fig. 3), and passing through the cortex reach the surface of the stem. When they traverse the sclerenchymatous sheath, they are accompanied with brown-walled sheaths, which gradually increase in thickness after the traces leave the stem.

E. Histological Structure of the Stem

According to the size of the stem, the dimensions of the different tissues vary. The following description is based on material with a diameter of 7 cm.

a. The Cortex

The epidermal layer of the stem peels off early, and the brown cortical layer under the epidermis, i. e. the hypodermal layer is exposed. The actual cortex, i. e. the part outside the stele, including the outer hypodermal layer, is not constant in thickness. It measures about one-tenth of the diameter of the stem, that is, 7–10 mm. in the stem 7 cm. in diameter.

The cortex may be divided into four layers. The first or outermost layer, or the brown hypodermal sheath, is a thin (about 1–2 mm.) but hard protective tissue surrounding the stem surface (Fig. 9, hy). The second layer is the widest region consisting of whitish parenchyma (Fig. 9, cor), in which many mucilage sacs are scattered (Fig. 9, ms). The third, most prominent characteristic sclerenchymatous sheath, with an average thickness of about 2 mm. (Fig. 9, sc), runs almost parallel to the stele. The fourth layer (Fig. 9, pa) is parenchymatous, and has the same thickness as the third, and numerous mucilage sacs are found in it.

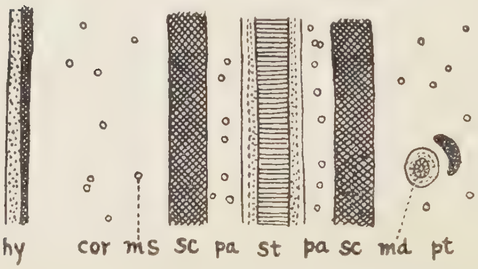

Fig. 9. Transverse section of the external part of a stem to show the general structure. (×3)

hy, hypodermal layer
cor, external cortex
sc, sclerenchymatous sheath
st, stele
pt, pith
pa, parenchyma
ms, mucilage sac
md, medullary bundle

The first layer is of brown colour and about thirty cells thick. The external one-third of this layer consists of parenchyma with a rather thick membrane, while the remaining two-thirds consist of sclerenchymatous fibers with the membrane of the same thickness as the former. The distinction between these two kinds of tissue is not clear in transverse section, though the cells of the former have a somewhat larger cavity than the latter, but it is apparent in longitudinal section. However, the transition between these two kinds of tissue is gradual. Cork is not developed.

The second and four layers consist of large parenchymatous cells, and embedded in both layers, especially in the fourth, mucilage sacs are abundant. In transverse section, these sacs are hollow circular cavities containing some mucilage, their diameter being somewhat greater than that of the surrounding parenchymatous cells (Fig. 10, A). They are

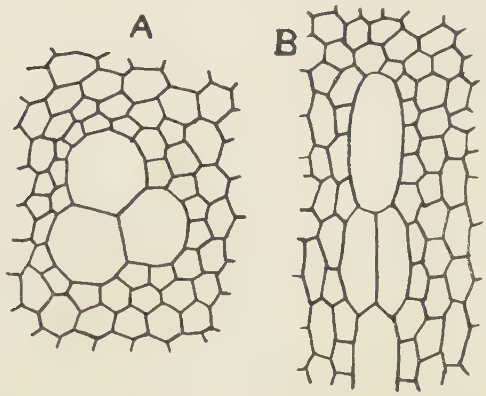

Fig. 10. Mucilage sacs in the fundamental tissue of the stem. (magnified)

A, Transverse section
B, Longitudinal section

solitary or in groups of two or three. In longitudinal section, it is seen that they are not canals, but are ellipsoidal sacs with rounded ends (Fig. 10, B). These sacs are arranged in an irregular longitudinal row.

The third layer, the characteristic sclerenchymatous sheath, consists of typical long sclerenchymatous fibers similar to those found in the inner half of the first layer. In the transitional region between these sclerenchymatous and parenchymatous layers, there is a layer of particular cells. In transverse section, they are similar to the fibrous cells, but in longitudinal section, they are quite different, because, these cells

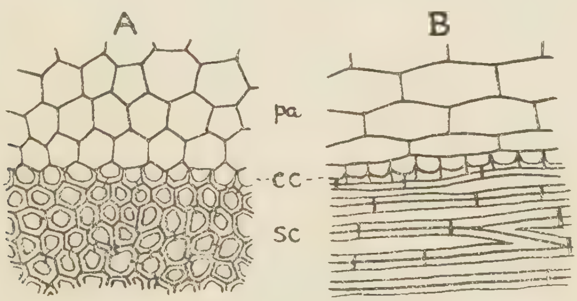

Fig. 11. Transverse and longitudinal sections at a part of the cortex to show the transition between parenchyma and sclerenchyma. (magnified)

A, Transverse section
B, Longitudinal section
pa, parenchyma
sc, sclerenchyma
cc, cubical cells

are not long fibers, but are very short and nearly isodiametrical, with thick inner and thin outer walls (Fig. 11). The presence of such cells has been recorded in the case of some higher plants[1] and also in ferns[2], but not in the Cyatheaceae. They may be called " cubical cells ".

b. The Stele

The stele is a hollow cylindrical tube with a wall about 2 mm. in thickness. In transverse section, each meristele is constructed according to the normal amphicribral type with a distinct endodermal layer (Fig. 12). Endodermal cells are elongated tangentially, and their radial walls distinctly show Caspary's points (Fig. 12, e). The pericycle is a parenchymatous layer of three or four cells thick (Fig. 12, per). The phl m consists of sieve-tubes and phloem-parenchyma (Fig. 12, ph). Sieve-tubes are distinguished from the parenchymatous cells by their greater size (Fig. 13, st). In the outer part of the phloem and in contact with the pericycle, there is a layer of protophloem, the cell-wall of which is crushed and swollen, as is ordinarily the case with the fern (Fig. 13, pp). In contact with the inner side of the protophloem-layer, there is seen, in transverse section, a layer of fairly large cells. These cells look like sieve-tubes, but in longitudinal section, it is clearly seen that these are not canals, but ellipsoidal sacs (Fig. 13, mc). They contain some mucilage like the mucilage sacs in the cortex, and swell so much that they press against the neighbouring cells. They may, there-

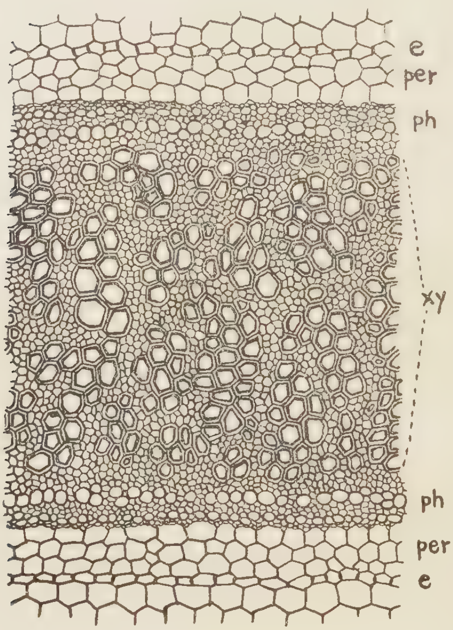

Fig. 12. Transverse section of the stele of the stem. (magnified)

e, endodermis ph, phloem
per, pericycle xy, xylem

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1) Payen (1842) Mémoir sur la dévelopment des végétaux. Paris; Treub, M. Observations sur la sclérenchyme. Versl. en Medd. Asd. Nat., R. 2, D. 11.

2) Mettenius, G. (1864)

fore, be called "mucilage cells". The presence of such cells was also described by SCHÜTZE (1906) in *Cyathea.* The sieve-tubes show the general fern-type, and small pit-areas are found on their radial walls. They are separated by one or two cell-layers of phloem-parenchyma from the layer of mucilage cells (Fig. 13). The conjunctive parenchyma, that is the parenchyma connecting the xylem and phloem, is a layer two or three cells thick. The phloem and endomermis on both sides of the xylem are of the same structure respectively.

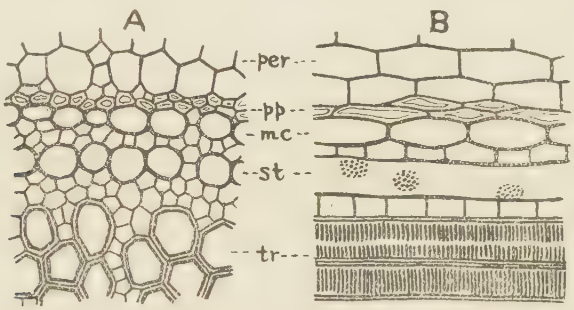


Fig. 13. Transverse and longitudinal sections through the phloem of the stele of the stem. (magnified)

A, Transverse section
per, pericycle
pp, protophloem
mc, mucilage cells
B, Longitudinal section
st, sieve-tube
tr, tracheids

The xylem occupies the central part of the stele and consists of a greater amount of tracheids and xylem-parenchyma (Fig. 12, xy). The size of the tracheids is not constant, but reaches 15 μ in diameter, and there is no regular order in their arrangement. They are all scalariform, and no spiral or annular ones are found, so that the position of the protoxylem is not distinct.

c. The Pith

The pith occupies the greater part of the center, and may be divided into three layers. The first is a parenchymatous layer bordering the inner side of the stele and corresponding to the innermost or the fourth layer of the cortex (Fig. 9, pa). The second is the sclerenchymatous sheath, which is continuous through the stelar gap to the similar tissue in the cortex (Fig. 9, sc). The third, the pith proper, enclosed in

the second or sclerenchymatous layer, consists of a large amount of parenchyma (Fig. 9, pt), containing mucilage sacs similar to those in the cortex, and also the medullary bundles (Fig. 9, md). Each of these layers is identical with that of the corresponding layers of the cortex in histological nature, and need not be described here; the medullary bundles are an exception and will be considered later.

d. The Leaf–Gap and Leaf–Trace

The base of the petiole is attached to the stem obliquely. The hard basal parts of petioles are left after the leaves are shed. These persisting bases consist of the hard peripheral layer and petiolar bundles, all of the fundamental tissue decaying off (Fig. 6). The decay of the parenchyma proceeds up to the stem surface, while there is a brown tissue like an absciss-layer or a diaphragm which protects the internal tissue against decay. Petiolar bundles penetrate this brown layer inwards, and project outwards into the hollow petiole.

In transverse section, the part of the stem at the absciss-layer is seen to correspond to a leaf-gap, that is the part where the pith and cortex are communicated with each other. The external layer of the stem on the absciss-layer just referred to is a thin brown layer, with the same appearance as the hypodermal layer, but its anatomical character is quite different from the latter; the absciss-layer consists of parenchymatous cells only, and contains neither fibers nor cork-tissue. The transition to the inner fundamental tissue is gradual. Indeed, at first, this is a part of the fundamental tissue between the stem and petiole, which, in the time of leaf-fall, becomes a diaphragm. The change to the diaphragm is accompanied by the thickening and colouring of the membrane and not by the cell-formation.

In transverse section of the stem, at the basal part of a leaf-gap there are semicircular grooves on the stem surface (Fig. 1, le). These are the lenticels situated at the very base of the petiole (Fig. 6). A lenticel consists of a fusiform groove, and tylosis-parenchyma is present not at all or only in a small quantity, because, in the lenticel of this plant the cork-cambium is not developed, differing from the typical one of Phanerogams, so that if the original cells once fall out, new ones will not be found in the groove.

The mode of parting and the arrangement of leaf-traces in a leaf-gap has been described above. The structure of every leaf-trace is similar, being as follows. In transverse section, it has a short, some-

what curved rod-shape. The endodermis is a distinct layer surrounding the bundle. The xylem is of almost the same form, but has a groove on the central inner side, where is situated the protoxylem. The phloem entirely encloses the xylem, with the protophloem in its periphery, and is separated from the endodermis by a layer of the pericycle, two or three cells thick. Internal protophloem is sometimes indistinct. The internal concave side of the xylem is occupied by the parenchyma and sieve-tubes. Inside the protoxylem, which is composed of spiral tracheids, is a large intercellular cavity, the protoxylem-cavity, which is commonly found in ferns. Outside the endodermis, there are brown sclerenchymatous bands, separated from the former by several layers of parenchymatous cells. It is seldom that these bands enclose the leaf-trace as a whole, but usually occupy the inner and outer sides, interrupted laterally. These bands are derived from the sclerenchymatous sheath of the meristele, when the trace traverses this sheath.

The above describes the normal leaf-traces, but they often present some irregularities due to the parting of root-traces, which occurs on the outer side of the trace.

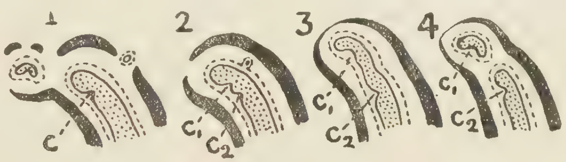
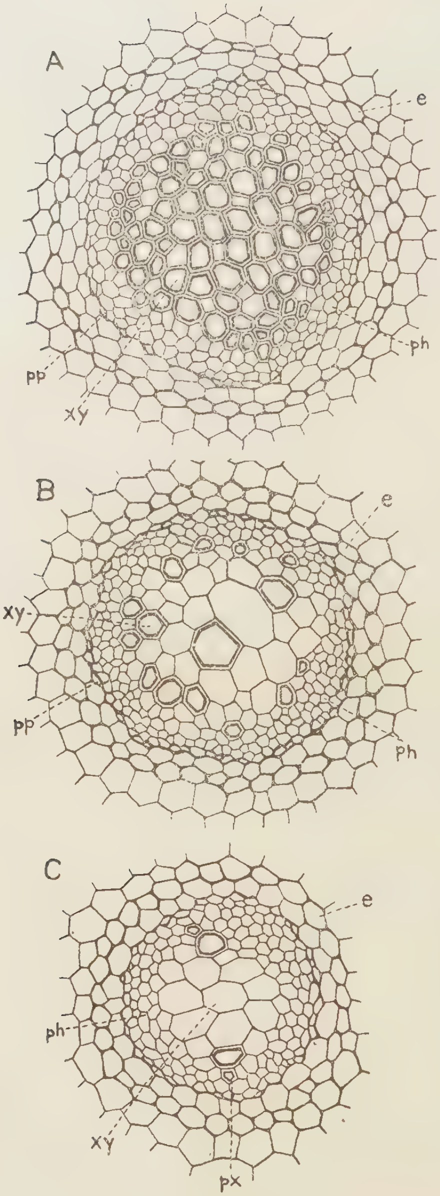


Fig. 14. Successive cross sections of a meristelic margin to show the process of formation of grooves of the xylem in the parting of a leaf-trace. A groove c bifurcates into two c_1 and c_2. (×2)

Next, the origin of the protoxylem in the leaf-trace must be traced, because, in the meristele itself there is no indication of protoxylem. When the marginal part of the meristele is about to be separated to form a leaf-trace, there appears, on the inner side of the xylem, at a short distance from the very edge, a small groove with a protoxylem and a large cavity (Fig. 14, 1, c). Prior to the parting of a leaf-trace, however, the protoxylem with the accompanying cavity on the margin of the meristele is bifurcated (Fig. 14, 2, c_1 c_2), and these two are gradually separated from each other (Fig. 14, 3). Of these two, the external one becomes the protoxylem and central cavity of the leaf-trace just about separate off (Fig. 14, 4, c_1). The inner one remains in the meristele (Fig. 14, 4, c_2), but it is soon bifurcated for the formation of the protoxylem of the next trace, and so on. Thus, on the marginal part of



Fig, 15. Successive cross sections at three levels of a root-trace. (magnified)

A, Near the place of parting
B, Middle part of the cortex
C, Outer part of the cortex
e, endodermis
ph, phloem
pp, protophloem
xy, xylem
px, protoxylem

the meristele, either one or two groups of protoxylems with accompanying grooves may be found.

The direction of each leaf-trace is caused by the outward curving of the meristelic margins, but in their structure they present no essential difference.

Leaf-traces traverse the cortex obliquely, and enter the petiole. In their course, the brown sclerenchymatous bands, which are accompanied with the traces when they penetrate the sclerenchymatous sheath of the meristele, diminishes gradually, and when the traces reach the external cortex, there remains only a small part, which entirely disappears in the base of the petiole.

e. The Root–Trace

Root-traces part from the meristelic margins of the leaf-gap, or from the basal parts of the leaf-traces themselves, and descend the cortex obliquely. The branching of a root-trace begins with the formation of a protuberance on the external part of the meristele. In the first place, an endodermal layer bulges out, and accompanying this, the phloem and xylem also bulge out in the same way. Then, the protruded xylem is constricted off from the main xylem, the phloem and endodermis follow the same process, and at last a distinct

small circular bundle, the root-trace, is established. In the case in which the trace part from the leaf-traces themselves, the same process takes place on the external side of the leaf-traces.

The root-trace thus parted is circular in transverse section, and its structure is of the protostelic type, that is, the central part is occupied by a circular xylem consisting of tracheids and a small amount of xylem-parenchyma, the xylem being enclosed in a ring of the phloem, which is enclosed in turn in an endodermal layer (Fig. 15, A). The differentiation of the protoxylem and metaxylem is not quite distinct.

In the oblique descent through the cortex, there occurs a certain change in its structure ; the greater amount of tracheids diminishes, and in consequence, the amount of xylem-parenchyma increases (Fig. 15, B). Still further downwards, the degenerating tendency of the tracheids becomes so pronounced that they are reduced to two small isolated groups, situated in the periphery on the opposite sides of the central parenchymatous cells (Fig. 15, C). Each group consists of only a few tracheids, of which the smaller ones representing the protoxylem are situated on the external side. Meanwhile, the size of the bundle itself gradually diminishes, and the phloem-elements also diminish, until at last, there remain only two groups, one on each side of the xylem-plate. Thus, a typical diarch bundle, a characteristic root-structure, is established in the middle part of the cortex of the stem (Fig. 15, C).

When a root-trace penetrates the sclerenchymatous sheath of the meristele, the sheath is interrupted forming a small hole (Fig. 3), and when the trace parts from the sheath, brown and thick-walled cells appear in the periphery of the trace, separated from the latter by several layers of parenchyma. These cells increase in amount when the parting from the sheath proceeds, and at last surround the trace as a thick ring. In the external cortex of the stem the ring of these brown cells encloses the root-trace completely, and between this tissue and the cortical tissue there is a distinct boundary. Thus, the formation of the root-trace is completed, the root being endogenous.

f. The Medullary Bundle

Medullary bundles which are distributed in the pith are of different sizes, reaching a diameter of 1 mm. They are usually circular in transverse section, but in some cases are elliptical. The larger bundle is accompanied by brown sclerenchymatous bands arranged in a ring, separated from the bundle itself by a parenchymatous layer. The

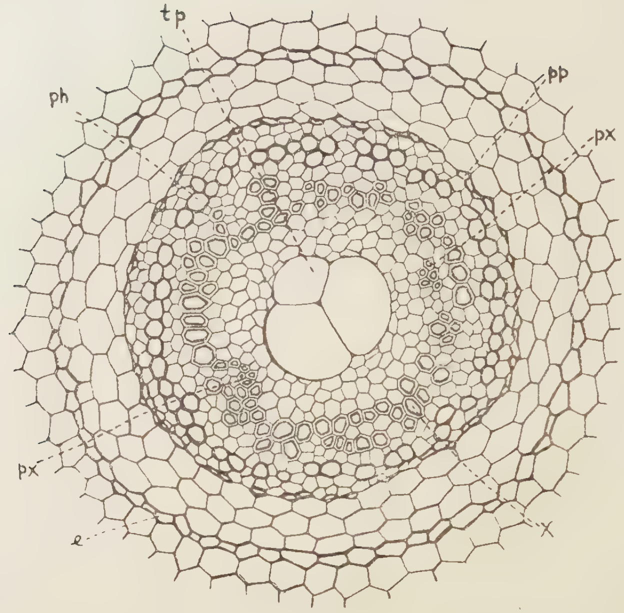


Fig. 16. Transverse section of a medullary bundle. (magnified)

e, endodermis
pp, protophloem
ph, phloem
xy, xylem
px, protoxylem
tp, tylosis-parenchyma

smaller bundle has one or two bands (Fig. 9, md), and the smallest none at all. This sclerenchymatous band corresponds to the sclerenchymatous sheath of the meristele, and has the same structure as the latter. There is also a particular layer of isodiametric cells in the transitional part between this sclerenchymatous tissue and the neighbouring parenchyma.

The medullary bundle itself is of the medullated protostelic type with an external endodermis (Fig. 16). Separated from the endodermis by a layer of the pericycle, is a ring of the phloem (Fig. 16, ph). The xylem also forms a ring on the inside of the phloem enclosing the central parenchymatous pith (Fig. 16, xy). The endodermis is a ring of a somewhat irregular shape, each cell clearly showing Caspary's points. The phloem is a narrow ring, on the outer side of which a protophloem-layer is situated (Fig. 16, pp). The xylem-ring consists of from one to three layers of tracheids, accompanied by a few xylem-parenchymatous cells. On the internal face of the xylem-ring, there are two or more groups of smaller annular or spiral tracheids. These groups, usually

two, project into the central pith, and indicate the position of the protoxylem (Fig. 16, px). They are sometimes separated from the ring of metaxylem by a parenchymatous layer, and in such a case, their position is very distinct. Neither the internal phloem nor endodermis are present. The central pith, enclosed in the xylem-ring, is variable in size. In smaller bundles, it is formed only of parenchymatous cells, but in the larger ones the central part is occupied by a large cavity, usually filled with large tylosis-cells (Fig. 16, tp). In some cases, the parenchyma in the pith contains small intercellular spaces, and the presence of various transitional forms, as seen in transverse as well as in longitudinal section, indicates that the central cavity is of a shizogenetic origin, and that the tylosis-cells are formed by the protrusion of surrounding cells into the cavity.

Now, the mode of union of the medullary bundle with the meristele is to be considered. When a medullary bundle approaches the margin of the meristele, the sclerenchymatous sheath of the latter is interrupted, and the sheath-margins thus formed are connected with the sclerenchymatous bands of the medullary bundle, thus making the sclerenchymatous sheaths of the meristele appear to curve outwards at the interrupted part (Fig. 17, 1). The medullary bundle penetrate this gate of the sclerenchymatous band, and approaches the meristele. At the same time, the margins of the opening of the sclerenchyma approach, and finally fuse with one another (Fig. 17, 2). Then, the medullary bundle unites with the meristele itself. At first, it is a protuberance, but gradually disappears (Fig. 17, 2–3). As the medullary bundle contains a central cavity and tylosis, in the case of fusion with the meristele, these tissues are incorporated into the meristele. When the protuberance of the meristele disappears, the cavity and its accompanying tylosis are entirely enclosed in the inside of the xylem. In this case, on the inner side of this enclosed cavity, there are one or two layers of tracheids, derived from the tracheids of the medullary bundle, which are distinguished by their smaller size. In this enclosed cavity, two groups of the smallest tracheids are often prominent; they are the direct continuation of the protoxylem-groups of the

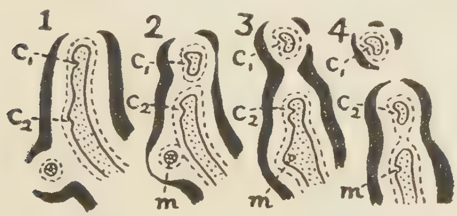


Fig. 17. Successive cross sections of a meristelic margin to show the process of formation of grooves of the xylem in the union of a medullary bundle. (×2)

c_1 c_2, grooves of the xylem
m, medullary bundle

medullary bundle. After a short time, the tracheidal layer on the inner side from the enclosed cavity diminishes, and soon disappears, so that the enclosed cavity is connected with the conjunctive parenchyma directly, forming a parenchymatous groove on the inner side of the xylem (Fig. 17, 3–4, m). This state is similar to the case of the groove of the xylem appearing, as above described, for the formation of a normal leaf-trace. Indeed, both kinds of grooves on the xylem are equivalent, and in this case also, the groove serves as a preparation for the parting of a leaf-trace. The leaf-trace thus formed becomes, as before stated, to some one of the superior series of petiolar bundles.

Now, there arises another question. As stated above, previous to the parting of a leaf-trace, a groove of the xylem bifurcates in the preparation for the next leaf-trace. In the present case, therefore, it is possible that the two grooves may appear in one leaf-trace, the one due to the bifurcation of the groove of the preceding trace, the other to the union of a medullary bundle. In fact, however, only one groove is found in each trace, because the groove of the preceding trace is not bifurcated and goes in that trace as a whole, leaving no groove on the remaining meristele, in which a new groove is formed by the union of the medullary bundle in the way described (Fig. 17, 1–4).

F. Histological Structure of the Leaf

a. The Petiole

The epidermis of a petiole is a layer of the thickness of one cell, the cell-membrane of which is rather thick and covered by a cuticle. Epidermal cells are of a long rectangular form in surface view, and no stomata are found. On the surface there are two kinds of hairs; the one scaly, and the other filiform, both brown in colour.

Inside the epidermal layer of the petiole, there is a layer consisting of several rows of large parenchymatous cells, followed by a rather thick layer of small sclerenchymatous fibers. The cell-membrane in both kinds of tissue is equally thickened and slightly coloured, manifesting a strong lignified reaction. These tissues are very hard, and may serve as a hypodermal sheath. The hypodermal ring envelops the whole of the petiole, being interrupted only by lenticels on the lateral sides.

Spines on the surface of the petiole are conical. The epidermis of the petiole continues to the surface of the spines, which are filled with small brownish thick-walled cells and contain no vascular system.

Lenticels penetrate deeply into the hypodermal layer. The inner border or the bottom of a lenticel consists of dark brown parenchyma, and gradually passes inwards to the cortical parenchyma. In the lenticel itself, brown rounded cells are arranged loosely, the tendency to which becomes more evident toward the external side, until finally some of the cells fall off. These loose cells correspond to the compensating cells of the lenticel in Phanerogams, but they are not quite equivalent to those of the latter, because they are not produced by the cork-cambium, but are the original parenchymatous cells themselves. In fact, in the basal part of the petiole, most of these cells fall out of the lenticel, and a fusiform cavity or groove is formed, which is not filled again.

The fundamental tissue of the petiole consists of large parenchymatous cells, in which the petiolar bundles and mucilage sacs are embedded. The latter are constructed in the same manner as those of the stem.

The form of the petiolar bundle varies at different levels in the petiole; in the basal part they are separated, each in a V-shape, while upwards they are united in a W or continuous wavy form. First, let us consider the structure of a V-shaped bundle. It is almost similar to that of a leaf-trace, but is onger and more curved than the latter (Fig. 18). A distinct endodermis encloses the bundle (Fig. 18, e). The xylem is of a V-shape, and both arms consisting of large tracheids curve slightly (Fig. 18, xy), and its central corner is occupied by many minute tracheids, or the protoxylem. An arm usually consists of one or two rows of large tracheids. In the parenchyma, in contact with the protoxylem, there is a lacuna, a protoxylem-cavity, sometimes with tylosis-parenchyma. The protoxylem and accompanying cavity of the petiolar bundle are direct continuation of the same tissues in the leaf-trace. The phloem encloses the xylem, and is of nearly the same thickness,

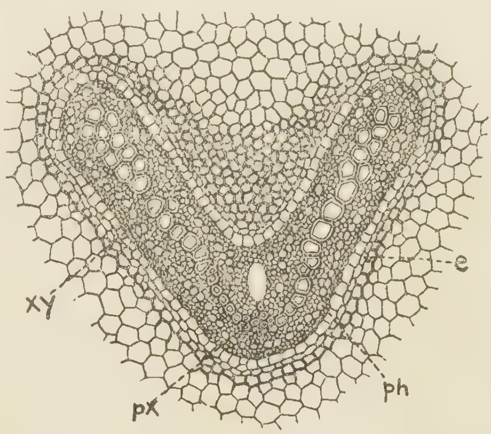


Fig. 18. Transverse section of a petiolar bundle. (magnified)

e, endodermis
pp, protophloem
ph, phloem
xy, xylem
px, protoxylem

but on the external side of the xylem-arms and near the protoxylem-cavity it is somewhat thicker (Fig. 18, ph). The protophloem is situated at the outer side of the phloem in a continuous layer, which is separated from the endodermis by one or two rows of pericyclic cells, but in front of the protoxylem-cavity, this layer is not distinct (Fig. 18, pp). The xylem consists of scalariform tracheids and xylem-parenchyma, while the protoxylem is composed of spiral or annular elements. The layer of sieve-tubes is separated from the xylem by a conjunctive parenchyma one or two cells thick. Mucilage cells, found on the inner side of the protophloem of the stem stele, are not found in the petiolar bundle; they disappear when the stelar margin is cut off from the meristele so as to form a leaf-trace.

Surrounding the endodermal layer, there is a protective sheath, which, contrary to the case of the stem stele, is in direct contact with the endodermis, and is not brown in colour. The sheath surrounds each bundle and is more abundant on the inner side of the V. It is a layer a few cells thick, consisting of long prosenchymatous fibers with thick and lignified walls. The transition of this fibrous layer to the fundamental tissue is gradual.

Next, let us briefly consider a wavy bundle. As the wavy form is a result of the mutual connection of V-shaped bundles, one wave corresponds to one original V. In the case of fusion, the xylem of each bundle fuses, and the phloem and endodermis also fuse into one another respectively, so that each tissue continues in a wavy form. The crest of the xylem-wave is occupied by a protoxylem, continued from that of a separate leaf-bundle.

b. The Rachis

The general structure of the rachis is similar to that of the petiole itself notwithstanding its smaller size. Uniseriate hairs survive for a long time, especillay on the upper part. Lenticels become smaller toward the end, and have a whitish appearance which is due to the presence of air between the epidermal layer and inner parenchymatous cells. The structure of the hypodermis, meristele and fundamental tissue is the same as that of the petiole.

c. The Lamina

The lamina or frond is of the normal fern-type. The epidermal cells have an irregular wavy outline in surface view, and contain a small quantity of chlorophyll-bodies, but they are rectangular on the nerves. Stomata are found only on the lower side.

The mesophyll consists of four or five layers of parenchymatous cells containing chlorophyll-bodies, and no distinct differentiation is found among these layers, though those of the lower side have larger intercellular cavities. The vascular bundle of the nerve is collateral in structure, and lacks a distinct endodermis.

G. Histological Structure of the Root

The roots have almost equal diameter ranging 1.0–1.5 mm. Their surface is covered while young with brown root-hairs, which usually fall off with age. Most of the roots are functionless, not reaching the ground.

The epidermis consists of one layer of parenchymatous cells. The cortex consists of outer and inner parts, the former consisting of parenchyma with thin cell-walls, and the latter of thick-walled long sclerenchymatous fibers. Epidermal and cortical cells have walls of a dark brown colour. The transition between the outer and inner tissue is gradual. The bundle is of the diarch radial type. The endodermis, a layer more or less distinct, is separated from the inner cortical fibrous cells by one or two layers of transitional cells. Internally, separated from the endodermis by one or two layers of pericyclic cells, are two groups of protoxylem, which consists of several small spiral tracheids. The metaxylem connecting these two groups consists of large tracheids arranged in one or two rows in a plate-form. The phloem is found on both sides of the xylem-plate, forming a normal root-type.

In most of the roots, the elements of the metaxylem show no histological differentiation, though they exhibit the form of tracheidal cells, their walls remaining thin and showing no characteristic pitting (Fig. 15, C). This is in accordance with the fact that most of the roots are functionless. This cessasion of the differentiation of the metaxylem occurs also in the root-trace itself, when the latter penetrates the cortex. In older roots, the central cylinder disorganises earlier than the cortical tissue; the roots become hollow, and so remain for a long time. The disorganisation of the root-stele extends up to the outer cortex of the stem, which is shown by small pits in cross section of the cortex.

II. The Young Plant

One of the chief objects in the study of the young plant is to explain the mode of origin of characteristic tissues found in the adult

plant, that is, of the stelar skeleton, sclerenchymatous sheath, and especially of the medullary bundle. For this purpose, the plants of 20–30 cm. in height were used.

A young plant, which was specially closely investigated and on which the following descriptions are chiefly based, had a stem about 30 cm. in height. Not only the subterranean part, which measured about 10 cm., but also nearly all other parts of the stem were clothed by a hard root-system so thickly that the stem itself was not exposed. The body of the stem tapered toward the top in a conical form. The upper part of the stem as well as the subterranean part was covered by half-decayed bases of petioles. Other plants collected showed similar features, though some irregularities were present in their shape.

The structure of this young plant was examined by successive cross sections of the basal part as far as 16 cm. from the basal tip. The sclerenchymatous sheath was neither so thick nor hard as in the adult plant. From the study of these sections, a stelar construction was determined, and the size and arrangement of leaf-gaps, the mode of branching of leaf-traces and root-traces, as well as the course and origin of the medullary bundle were made clear.

A. Cross Sections of the Stem

Before describing the stelar construction thus determined, it will be convenient to give a description of the six main parts.

Region A (the tip; diameter 6 mm.; Fig. 19, A). The tip of the conically tapered stem base has a diameter of about 4 mm., but the true tip has been lost by decay. Even this stem base is covered by persisting petiolar bases. In transverse section of the tip, the detailed structure is hardly recognizable, bacause this part is very dark brown, being half-decayed. However, the inner structure is well preserved at the part about 1 mm. above the tip. Here, in the region A, the outline of the stem in transverse section is almost circular with a diameter of about 6 mm. Exposed on the surface, there is a brown tissue, and embedded in the fundamental tissue, which follows the latter, are two bands of meristeles, running parallel to each other, each enclosed by a thin sclerenchymatous band. At the elongated stelar margins in one of the two leaf-gaps, two small bundles, the leaf-traces, are seen. The bulging part of the stem, in which the leaf-traces lie, presents a leaf-base. The pith or the central fundamental tissue lying between the two sclerenchymatous bands is narrow. No medullary bundle is present.

Root-traces are found near the leaf-gap. Thus, the stele in this region shows that the leaf-gaps are overlapping, so that the stele itself is a dictyostele. This form of structure is the lowest part of the stem actually known in this young plant, but judging from the facts known in other ferns, especially in the sporelings of the Cyatheaceae described by some authors,[1] it may be assumed that the very tip is constructed after a protostelic type, but further upwards, a solenostele and then a dictyostele are to be found.

Fig. 19. Transverse sections of six regions of the stem of a young plant. (nat. size)

A, Region A D, Region D
B, Region B E, Region E
C, Region C F, Region F

Region B (15 mm. above the tip; diameter 10 mm.; Fig. 19, B). In this region, where the diameter of the stem is larger, the bases of petioles are preserved. A cross section of the stem in this region presents a triangular shape with rounded corners, owing to the bulging of the petioles. The diameter of the stem is 10 mm. and that of the stelar ring 6 mm. Exposed on the surface, there is a thin brown sclerenchymatous hypodermis. The stelar ring makes a triangular shape, whose sides are almost parallel to the stem surface, and the meristeles, two larger and one smaller, show that the phyllotaxy is $\frac{2}{5}$. Outside the leaf-gap, two pairs of leaf-traces are seen. Each meristele is enclosed by a brown sclerenchymatous band. The base of a petiole is relatively large, on account of

1) Chandler, S. E. (1905); Stephenson, G. B. (1908); Gwynne-Vaughan, D. T. (1901–03).

which the outline of the stem is angular. In the pith, which is also triangular, seven small medullary bundles are found. They are not accompanied by sclerenchymatous masses.

Region C (30 mm. above the tip; diameter 18 mm.; Fig. 19, C). This region is, in transverse section, of an irregular triangle with rounded corners, though it is more circular than the region B. It has a diameter of about 18 mm. An ordinary brown sclerenchymatous sheath covers the whole of the stem surface. The stelar ring, about 12 mm. in diameter, is interrupted at three points, showing its phyllotaxy to be $\frac{2}{5}$. In a leaf-gap three pairs of leaf-traces are found, and from its margins root-traces are also given off. The pith becomes larger and more circular, and contains nine medullary bundles, some of which accompany a small amount of sclerenchymatous tissue.

Region D (60 mm. above the tip; diameter 24 mm.; Fig. 19, D). A transverse section of this region shows a triangular form with rounded corners. The diameter of the stem is 24 mm. and that of the stele 17 mm. The internal structure coincides with that of the preceding region. Four pairs of leaf-traces are found in each gap, and the medullary bundles are twelve in number. In other points, no peculiarities are found.

Region E (105 mm. above the tip; diameter 30 mm.; Fig. 19, E). In cross section, the outline of the stem of this region is also triangular with the diameter of 30 mm. Five or six pairs of leaf-traces are found in a gap. The stelar ring is also triangular with a diameter of 21 mm. In the internal structure no particularly interesting points are seen. A slight curving of the stelar margins in the leaf-gap, the typical Cyatheacean type, is noticeable. Nineteen medullary bundles are found.

Region F (165 mm. above the tip; diameter 35 mm.; Fig. 19, F). This region shows a more circular outline than the preceding, having a diameter of 35 mm. There are six or seven pairs of leaf-traces in each gap, and nineteen medullary bundles in the pith. The stele, 25 mm. in diameter, is constructed after the dictyostelic type with a phyllotaxy of $\frac{2}{5}$. In other points, no particular differences to the preceding are found. The curving of the gap-margins and the mode of branching of the leaf-traces are similar to the type in the adult plant.

B. Solid Construction of the Stem

Now that the descriptions of six main different regions have been given, we enter on the reconstruction of the solid structure of the stem.

a. The Stele

The diameter of the stelar ring increases in proportion with that of the stem. The relation of the distance of a region from the tip and the diameter of the stem and stelar ring in that region is as follows :

Region	A	B	C	D	E	F
Distance from the tip (mm.)	1	15	30	60	105	165
Diameter of the stem (mm.)	6	10	18	24	30	35
Diameter of the stele (mm.)	2	6	12	17	21	25

The rate of increase of the diameter of the stelar ring diminishes from the conically tapered tip of the stem base toward the upper part of the stem. In a graphic representation, if we take x for the distance of a region from the tip and y for the semicircumference in that region, the curve to show the rate of increase of the circumference may be expressed by the parabolic formula $y^2=px$, where $p=10$. A graphical representation of the stem stele developed according to this formula is given in Fig. 20.

b. The Leaf-Gap

At the very tip of this material are located two leaf-gaps. By serial sections of the stem, the position or arrangement of leaf-gaps along the stele and the size of each gap can be ascertained, and these are shown diagrammatically in the Fig. 20.

In the first place, the change in the size of the gaps will be considered. The gaps have different sizes according to the size of the stelar ring, being larger in the upper part than in the basal part of the stem. They are long and fusiform, like those of the adult plant. The vertical length as well as the longitudinal breadth of the gaps at different levels changes according to the rate shown below, where only the length in six main regions is recorded :

Region	A	B	C	D	E	F
Length of the gap (mm.)	4–5	6–8	10–12	15–18	20–25	26–30

Next, the distribution or mutual arrangement of the gaps will be considered. We have traced 41 gaps in the stele, and their mutual relation has been determined (Fig. 20). At the tip of the material, only

two gaps are found, while throughout the whole length of the stem three gaps, and sometimes four, are found in one and the same transverse section, that is, three or four gaps overlap one another (Fig. 19). Three gaps are not equal distances apart from each other, and from their position it is easy to determine, even by a transverse section, that the phyllotaxy is $\frac{2}{5}$. But, strictly speaking, it is not exactly $\frac{2}{5}$ throughout the stem. In the basal region, the sixth gap is situated just above the first, while in the upper region the arrangement undergoes some slight change, in consequence of which, the orthostichies derived from connecting the corresponding gaps are not vertical, but twisted in a spiral. This tendency becomes more pronounced toward the upper part; consequently, a $\frac{3}{8}$ phyllotaxy may result. As a matter of fact, on the upper part of this young plant, the phyllotaxy may be considered as $\frac{2}{5}$ on the one hand, and as $\frac{3}{8}$ on the other hand, because the orthostichies derived from $\frac{2}{5}$ and $\frac{3}{8}$ have almost the same inclination to the vertical line, though their inclinations are opposite (Fig. 20). It is interesting to notice here that, the phyllotaxy in the adult form of this species is $\frac{3}{8}$, and may be considered that, the region between A and F is the transitional part between $\frac{2}{5}$ and $\frac{3}{8}$. The phyllotaxy can be also determined by means of the arrangement of the petioles, but as the surface undergoes some decay, it is not easy. The change of the phyllotaxy in one and the same plant is not a rare phenomenon, and many cases were recorded by SCOTT (1874) in some Cyatheacean plants. One of the largest plants collected in the Island of Hachijô has a phyllotaxy of $\frac{3}{8}$, while in those from other localities, the more advanced phyllotaxy can be seen.

Another fact must be here recorded. The phyllotaxy in this young plant is left-handed, while that of the adult plant is right-handed. The latter form is the normal type and the former an exceptional one. Such an opposition in the orientation of the phyllotaxy in one and the same species was found also by the writer in the rhizomes of *Athyrium nipponicum*.

c. The Leaf-Trace

Accompanying the increase of size of leaf-gaps from the base of the stem upwards, the number and the mode of branching of the leaf-traces in each gap undergo a gradual change. In a transverse section of the stem, the petiolar base is cut obliquely, and the exact arrangement of the petiolar bundles cannot be seen. Accordingly, for the present purpose, the writer has compared other young materials.

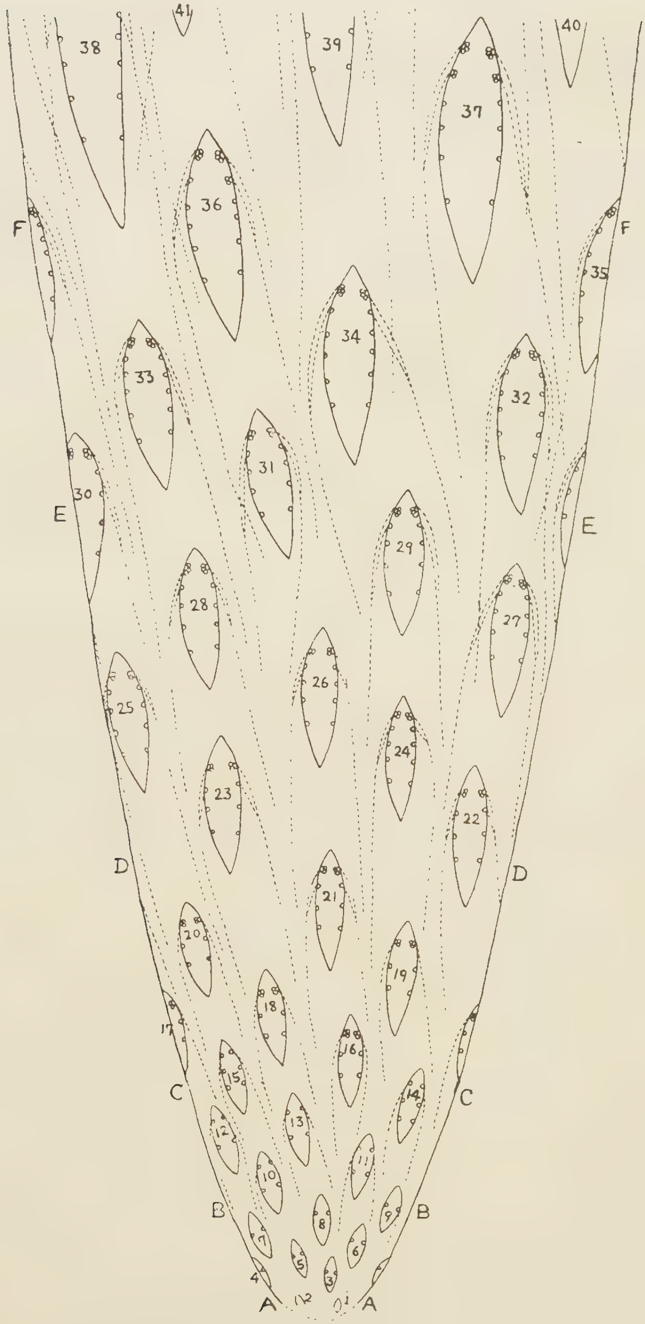


Fig. 20. Developing figure of the stele of a young plant showing the arrangement of leaf-gaps (1—41), the mode of branching of leaf-traces (small circles), and the origin and course of the medullary bundles (dotted lines). A—F show the six regions in text. (nat. size)

In the first place, the number of leaf-traces must be considered.

In the lowest part, only one pair of leaf-traces is seen. This state is maintained until the ninth gap, while in the tenth and following gaps there are two pairs, and in the fourteenth there are three. Thereafter, the number of traces increases gradually as is shown below, in connection with the increasing transverse diameter of the petiolar bases:

Region	A	B	C	D	E	F
Diameter of the petiole (mm.)	4	6	8	10	12	18
Number of leaf-traces (in pairs)	1	2	3	4	5–6	6–7

In the upper parts of the stem, the number of leaf-traces becomes inconstant, because some of the traces bifurcate or trifurcate as soon as they are parted from the gap, and the number of parted traces and that of the petiolar bundles do not coincide. One of the upper gaps of this young plant has eight pairs of traces and eleven pairs of petiolar bundles.

Now, the mode of parting of the leaf-traces will be considered. The position and order of parting differ considerably according to the size of the gaps and the number of the leaf-traces, so that we must consider them according to their respective parts of the stem.

Region A (one pair of leaf-traces). In the case of one pair of leaf-traces, the mode of parting coincides with that of the Polypodiaceae, that is, a trace is costricted from the stelar margin at the gap which projects externally. On entering the petiole, the two bundles are situated on the external side. The parting takes place in the middle or somewhat above the middle of the gap.

Region B (two pairs of leaf-traces). In a petiolar base with a diameter of 6 mm., four bundles are arranged at equal distances on the periphery, two externally and the other two internally, all facing the center of the petiole (Fig. 21, A). The mode of parting is almost the same as in the preceding case, that is, the first pair parts from the projecting margins of the gap, and the second follows in the same way. Both of them are parted from the upper half of the leaf-gap. A pair of medullary bundles is combined with the second pair of traces (Fig. 20).

Region C (three pairs of leaf-traces). Here, the petiole with a diameter of 8 mm. has four pairs of petiolar bundles, while there are three pairs of corresponding leaf-traces. This difference is due to the bifurcation of one of the traces. Three pairs of leaf-traces, external, lateral and internal, are arranged in a ring at the very base of the petiole. Some-

what higher up, the lateral pair twists to the external side, and with the external one forms the superior series, while the internal pair soon bifurcates and becomes the inferior series (Fig. 21, B). The mode of parting of each trace is almost the same as in the preceding case, but the curving of the stelar margins now begins. The margins of the gaps extend externally, and the first pair of the traces is parted from their ends. The gap becomes broader, its stelar margins curving outwards, and then the second pair is given off from the margins. Then, the gap becomes narrower, where a pair of the medullary bundles fuses, and from the margins the last pair of the leaf-traces is given off. Somewhat later, the gap closes.

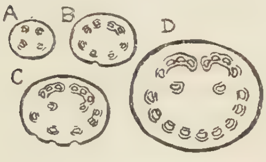


Fig. 21. Transverse sections of petiolar bases in four different parts of a young plant showing the change in the arrangement of vascular bundles. (nat. size)

A, Region B
B, Region C
C, Region D or E
D, Region E or F

Region D or E (four or five pairs of leaf-traces). The number of leaf-traces in this region with a petiole of about 12 mm. in diameter, is more inconstant owing to the fact that, on the one hand, the traces parted from the margin of the gap are not always in pairs, and on the other hand, the traces bifurcate as soon as they are parted from the meristele. For example, though there are six pairs of bundles in the petiole, there are only four pairs of parting traces. In this case, in the petiolar base six pairs of bundles show a different arrangement to the preceding, that is, two pairs are situated on the external side and three pairs on the internal side close to each other, while there is another pair on the lateral side projecting somewhat inside the elliptical ring formed by the former five pairs (Fig. 21, C). This pair belongs to the laterally projecting bundles of the superior series, and forms with the three internal pairs the superior series; the two external pairs on the other hand belong to the inferior series. After the first pair is given off, the gap becomes broader, and the margins begin to curve outwards, and from there the second pair is parted. Then, the margins recover their former curvature, and the third pair is parted inwards corresponding to the laterally projecting pair, to which a pair of medullary bundles is attached. The gap now becomes narrow, and its curved margins are cut off, and become the last or fourth pair. The latter usually trifurcates, and forms six pairs of petiolar bundles. With the last pair, there is combined another pair of medullary bundlles (Fig. 20). Thus, the mode of parting of the leaf-traces in this region shows clear signs of the characteristic features of the adult plant.

Region E or F (six or seven pairs of leaf-traces). In this region there are almost six or seven pairs of leaf-traces, while in the petiole, which are 20 mm. in diameter, there are ten pairs of bundles, of which nine pairs are arranged near the surface in an elliptical ring, while another pair is lateral and projects somewhat inwards (Fig. 21, D). Five lower pairs belonging to the inferior series are separated more or less from one another, while four inner pairs of the superior series approach one another. The mode of parting of the leaf-traces from a gap is almost the same as that in the former case. After it has opened the gap broadens gradually, and in its course four lower pairs are given off successively. During this process, the margins curve outwards, and then, after the parting of the fifth pair they begin to recover. From the recovering margins is parted the sixth pair, which corresponds to the laterally projecting one. The ends of the meristele curve outwards again, and the seventh pair is given off, while the remaining parts are parted as the eighth pair, which soon trifurcates. Two pairs of medullary bundles are joined to two pairs of leaf-traces (Fig. 20).

From the above statements concerning the mode of parting and the arrangement of the leaf-traces, the difference of this plant from most of the Polypodiaceae is quite clear. Though in the case with one pair of traces they are similar to the Polypodiaceae, in the case with two or more pairs, the traces are arranged in a ring in this plant, while in the Polypodiaceae they are in an arc with the opening upwards. The circular arrangement of petiolar bundles in the Cyatheacean plants is caused by the characteristic curving of the stelar margins of the leaf-gaps, the tendency to which appears at the level where three or four pairs of leaf-traces are given off. At the same time, the laterally projecting bundles appear, and this tendency becomes more pronounced higher up. This lateral projection begins in the bundles belonging to the superior series, while that of the inferior series does not appear in this young plant, but does appear somewhat later on. The bifurcation or trifurcation of the last trace after its parting begins at the gap with three pairs of traces.

d. The Medullary Bundle

In the basal part of the stem of the young plant, no medullary bundles are found. They first appear in the region 12 mm. above the tip, or a little below the region B. In this region, one or two small bundles appear in the pith independently of each other as well as other

bundles. Tracing the stem upwards, the number of medullary bundles gradually increases as is shown below:

Region	A	B	C	D	E	F
Number of medullary bundles	0	7	9	12	19	19

Tracing the medullary bundles upwards, we find that they ascend through the pith, and finally fuse with the margins of the leaf-gaps. In details, however, their behavior differs in various parts of the stem.

In the first place, let us consider the medullary bundles between the regions B and D, in which only one pair of medullary bundles is related to one gap. Appearing at a certain level, a bundle runs through the pith up to the sixth gap above the level, and here fuses with the margin of the gap. The medullary bundles always appear in the neighbourhood of a gap, and behave in the same way throughout their course. As the phyllotaxy of this young plant is almost $\frac{2}{5}$, the sixth gap belongs to the same orthostichy as the first. Thus, it may be said that a pair of medullary bundles appearing at a level fuses with the gap belonging to the same orthostichy. This relation is maintained throughout the stem. The length of a medullary bundle, therefore, depends on the distance between two successive leaf-gaps belonging to the same orthostichy (Fig. 20). Next, let us take the bundles between the regions D and F. They follow the same course as those of the preceding regions, but with the difference that, before the fusion of a bundle with the meristele, it bifurcates and a branch fuses with the stelar margin in the middle part of the gap, while the other branch fuses with the stelar margin at the top of the same gap. The bifurcation of medullary bundles begins with the pair which appears near the sixteenth gap and fuses with the twenty-first gap (near the region D). All of the bundles belonging to the gap above the latter bifurcate and fuse respectively in the same way (Fig. 20).

The first eight gaps at the stem base are not connected with any of the medullary bundles. The first bundle appears near the fourth gap and fuses with the stelar margin on one side of the ninth gap, the second bundle appers near the fifth gap and fuses with the stelar margin on one side of the tenth gap, and in the gaps above the eleventh, one pair of medullary bundles fuses with the margin, while from the twenty-first gap upwards, two pairs of branches of one pair of medullary bundles fuse with a gap. In rare cases, a medullary bundle trifurcates,

and one of the resulting three branches fuses with the middle part of the gap, the second fuses with a part at some distance above the former, while the third runs up to the top of the gap, and there it fuses with the margin.

The bundles maintain this course throughout the stem of this young plant, and it seems to be maintained in the adult plant too. The relation in the latter is, however, so complex that it is difficult to trace each of the medullary bundles throughout its entire course.

As before mentioned, the leaf-gap becomes larger in the upper portion of the stem, the interval between successive gaps in the same orthostichy becomes greater, and the individual bundles themselves also become longer as in the following scale:

Region	A	B	C	D	E	F
Length of the medullary bundle (mm.)	—	17	35	65	90	105

The places where the medullary bundles fuse with the margins of the gap are constant. In the regions between B and D, where two or three pairs of leaf-traces are parted from a gap, it is at the very base of the last pair of traces that a pair of medullary bundles is combined with the traces. In the regions above D, there are more than four pairs of leaf-traces belonging to a leaf-gap, of which at least two pairs belong to the superior series. In these regions, a medullary bundle bifurcates before the fusion, and one of the branches fuses with the first leaf-trace of the superior series, and the other with the last trace. It is of interest that the margin of the first gap having two pairs of leaf-traces of the superior series (twenty-first gap) is combined with the branches of medullary bundles bifurcated for the first time. In the case of trifurcated medullary bundles, the middle branch fuses with one of the superior series.

The case in the adult plant seems to be similar to that in this upper region of the young plant, which may be considered as a transitional region.

e. The Root-Trace

The mode of parting of root-traces is not so important, as it coincides with that of the adult plant. They are parted from the lower half of each gap. Of course, they are fewer in number in the lower smaller gap than in the upper larger one.

C. Histological Structure of the Young Plant

The histological structure of the stem and leaves is almost the same as that of the adult plant, and no special statement seems neccessary.

In short, the stem is covered with a brown hypodermal layer, and each meristele is enclosed by the sclerenchymatous sheath. The meristele itself is concentric. Of course, as the size of the stem varies in different parts of the stem, so the size and number of the tissue-elements vary in different regions. The following are some examples:

Region	A	B	C	D	E	F
Thickness of the xylem (μ)	20–30	30–36	40–50	45–55	50–60	55–65
Diameter of tracheids (μ)	2–4	4–6	4–6	6–8	6–8	7–8
Thickness of the sclerenchymatous sheath (μ)	20	25	30	40–50	40–60	40–65
Diameter of pith-cells (μ)	8	10	9	10–14	12	12
Diameter of the medullary bundle (μ)	—	15	15	25–30	30–35	30–40

It may now be worth while to describe the structure of the medullary bundle. At the region B, it is small and is constructed after the protostelic type, consisting of only a few tracheids surrounded first by the phloem, and then by the endodermis consisting of about twelve cells. Upwards, the tracheids of the xylem increase to ten or more, and higher up, parenchymatous cells appear within the tracheidal mass. In these cases, various transitional forms are seen. The lower end of the bundle appears independently in the pith. At the extreme end, the tracheids are very short and of the parenchymatous cell-form, though they show the typical scalariform pittings. The endodermis extends to the very end of the bundle.

Summary

1. The stem of *Cyathea spinulosa* is erect and of uniform diameter throughout, though toward the lower end it tapers in a long paraboloid form. The size of the leaves varies according to the size of the stem. The roots, springing from the petiolar base, are short, only those on the basal part of the stem reaching the ground. The bases of the petioles and roots persist for a long time, and cover the stem, thus serving as a protective sheath.

2. The phyllotaxy changes at different levels even in one and the same plant. In the basal or younger part it is $\frac{2}{5}$, and changes gradually upwards, until in the adult part it is $\frac{3}{8}$, or even more advanced. The phyllotaxy is usually right-handed, but exceptionally may be left-handed.

3. The surface of the stem is covered by a brown protective tissue, the outer half of which consists of thick-walled parenchyma, and the inner half of sclerenchymatous fibers. Both kinds are primary tissue and not the product of a cork-cambium. The epidermis is lost usually in early stage.

4. The stele of the stem is of the normal dictyostelic type overlapping three (in the young plant) to five (in the adult plant) gaps at one level. Each meristele is enclosed in a brown sclerenchymatous sheath. Leaf-traces are given off from both stelar margins of each gap which curve outwards, and root-traces from both margins of the lower half of each gap or from the very bases of parting leaf-traces.

5. The meristele is constructed after the normal fern-type, that is, the amphicribral concentric type. The xylem consists of large scalariform tracheids and parenchyma, spiral or annular tracheids being absent. The latter form of tracheids is found, however, in the marginal regions of the meristele, which are about to part as leaf-traces. In the external part of the phloem there is a layer of the protophloem, in contact with which is a row of 'mucilage cells'. The endodermis is distinct.

6. The sclerenchymatous sheath entirely encloses the meristele, and is separated from the latter by a parenchymatous layer. The sheath consists of fibers, and in the transitional part between this layer and the parenchyma, there is a layer of small 'cubical cells', whose membrane is thick on the sclerenchyma-side and thin on the parenchyma-side. The fundamental tissue is parenchymatous, and in it there are many 'mucilage sacs'. In the pith, there are numerous medullary bundles, of which the larger ones are accompanied by small sclerenchymatous masses. The number of medullary bundles is few in the young part, and is numerous in the adult, forty to fifty being found in a transverse section.

7. The leaf-gaps are small in the young or basal part of the stem, and become gradually larger upwards. A leaf-gap is long-fusiform with curved margins. Leaf-traces part from both stelar margins of the leaf-gap, usually in pairs. The parting points of the traces are further apart in the basal part of a leaf-gap than in the upper part, where successive

traces almost touch one another. The traces parted from the lower part of a gap belong to the 'inferior series', and those from the upper part to the 'superior series'. In the young plant, the parted traces are fewer in number, and the mode of branching is simpler.

8. The petiole is circular or elliptical in a transverse section. Beneath the epidermis, there is a continuous layer of sclerenchymatous fibers and petiolar bundles, and a small quantity of mucilage sacs is found in the fundamental tissue. On the surface of the petiole and rachis, especially on the lower side of the petiolar base, there are hard conical spines, and on the lateral sides there are lines of fusiform grooves corresponding to lenticels. The leaves are covered with scaly hairs in their younger stages.

9. The number of petiolar bundles differs considerably according to the age or size of the petiole, the adult sometimes containing fifty strands. The arrangement of the petiolar bundles is characteristic; they are disposed in a circular form almost parallel to the surface of the petiole, and in addition to these, two rows of bundles project inwards on the lateral sides, and on the upper side two or three bundles also project inwards. The upper half of the peripheral ring and the upper row of the laterally projecting series, including also the upper projecting strands, belong to the 'superior series', while the lower half of the ring and the lower rows of laterally projecting strands belong to the 'inferior series'. In the younger petioles, the arrangement is similar though the parts are simpler.

10. Each bundle of the petiole is V-shaped, and the direction of these bundles is definite in both series. This is caused by the outward curving of the meristelic margins.

11. On tracing the petiolar bundles upwards to the rachis, these separate V-shaped bundles are seen to fuse into each other gradually, until they form four wavy bands, of which the upper two belong to the superior series and the lower two to the inferior. Still higher up, two bands in each series are also combined so as to form two bands. Thus, though the bundles belonging to the superior and the inferior series are combined in one band in each series, both series do not fuse until the very end of the rachis, in which, for the first time, the two bands are combined into a single bundle.

12. In the case of branching of the pinnae from the rachis, the pinna-traces, which are two to four in number, are formed by the constriction of both series of rachis-bundles respectively. Thus, each series of pinna-traces is a direct continuation of the corresponding series of

the rachis-bundles. The two series run through the pinna independently, until at the very end of the pinna they fuse into one. In the branching part of the pinna-traces, a small connective strand connects both series.

13. A petiolar bundle is V-shaped in cross section, and the xylem is also of the same form, and in the inner angle is situated a protoxylem accompanied by a cavity. The phloem entirely encloses the xylem, and is in turn enclosed by an endodermis. On the external side of the endodermis there is a layer of sclerenchymatous fibers, especially developed in the inner angle of the bundle.

14. The lamina consists of several layers of assimilating cells. The foliar bundles or nerves are collateral. Stomata are found in the lower side.

15. The roots often branch, and in the younger stage they are covered by brown root-hairs. In the cortex, a thick layer of sclerenchyma is found. The stele is of the normal diarch type, and in some cases metaxylem-elements are not well differentiated, though they have the tracheidal forms.

16. The medullary bundles are of a typical protostelic or medullated protostelic type. In the latter case, parenchymatous pith with a cavity containing tylosis-parenchyma is found in the xylem, and usually two groups of the protoxylem are seen. The endodermis is distinct.

17. The medullary bundles appear in the pith and ascend through the latter as far as to the basal part of the leaf-traces belonging to the superior series. Before the fusion, they divide into a few branches, and the first branch fuses with the first trace of the superior traces, the last branch with the last, and the intermediate branch, if present, with one of the intermediate traces. The upper projecting leaf-traces are direct continuations of the medullary bundles. The total length of a medullary bundle corresponds to the distance of consecutive leaf-gaps in the same orthostichy ; consequently, it is shorter in the younger stage and becomes longer in the adult.

18. Considering all these points, the medullary bundle of this plant has a different origin from that of the polycyclic steles found in some ferns, so that the stelar type of this plant seems to be a different one. For the sake of convenience, this stelar type may be called a " Cyathean Dictyostele ".

III. Alsophila Ogurae, Hayata*

In a trip to the Bonin Islands, made in January 1925 to obtain material for the anatomical study of the Cyatheaceae, the writer collected, in addition to the well-established species, *Alsophila Bongardiana* and *Cyathea spinulosa*, a species of *Alsophila* which seemed to be new and rare. A part of the collection of this plant was handed over for taxonomic determination to Professor HAYATA, who named the plant *Alsophila Ogurae*, a new species.[1]

This plant is not so abundant in the Islands as the other two species just referred to. The writer found it in two places on Chichi-jima (Father Island), one of the Islands situated in latitude 27° 5′ N. and longitude 142° 10′ E. In one of two localities, several plants were growing together with two other kinds of tree-ferns. This species is easily distinguishable by its smaller and more slender statue from the others.

I. The Adult Plant

The stem of the adult plant is erect and reaches 2–3 meters in height. The leaves are limited to the top of the stem, the older ones falling off from their basal attachment. Adventitious roots spring from all sides of the stem and closely cover its surface and leaf-bases as well. Therefore, the diameter of the stem itself cannot be estimated exactly from the outside. Its real diameter reaches 6–7 cm. in the thickest specimens.

A. Structure of the Stem

The solid construction of the stem was studied by a comparison of its serial cross sections. It shows a typical Cyatheacean construction.

The general outline of a cross section of the stem is circular, with a number of protuberances at the attachment of the petioles (Fig. 22).

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* The contents of the Part III appeared in Japanese in the Bot. Mag. Tokyo, Vol. 39, pp. 197–214, July 1925.

1) HAYATA, B. (1925) Alsophila Ogurae, a new species of tree-fern from the Bonin Islands, together with notes on the Cyatheaceae found in the same group. Bot. Mag. Tokyo, Vol. 39, pp. 149–151.

The diameter measures 6–7 cm. On the outermost part there is a thin brown protective sheath, immediately within which is a region of white parenchyma. Next to the latter, there is the ring of the stelar body divided into several segments (Fig. 22, st), each of which is enclosed by a brown sclerenchymatous sheath (Fig. 22, sc). Thus, the general structure of the stem is similar to that of *Cyathea spinulosa*, and therefore, the structural points different from the latter species will be chiefly described below. The internal structure of the stem was studied by a comparison of successive cross sections of a stem with a diameter of 6–7 cm., through a length of 7 cm.

a. The Stele

The stele of the stem is a tubular cylinder, the wall of which is perforated by many leaf-gaps. In a transverse section, there are usually five gaps, though four or six are occasionally found. Judging from the position of the gaps (Fig. 1, A–J) the phyllotaxy seems to be nearly $\frac{3}{8}$. It is, however, more complex. This relation coinsides with the result obtained by a consideration of the arrangement of the leaf-scars. It is to be noticed that the phyllotaxy of this plant is not constant, but differs considerably in different individuals as well as at different levels in the stem of one and the same individual. Moreover, the phyllotaxy is either left- or right-handed. Besides, some irregularities occur in the arrangement of the leaves; in one case, it has been ascertained that this irregularity is due to the division of one gap into two.

The meristele is thin, and its marginal part curves outwards considerably, so that, in cross section, a narrower meristele shows a semicircular shape, while a broader one has the central part curved outwards so as to form, as a whole, a wavy contour or a W-shape. This central projection corresponds to the closed part of the lower leaf-gap or to the beginning of the upper gap (Fig. 22, F–I). One of the gaps in this material measures about 6 cm. in length. There are no gaps on the stelar wall other than leaf-gaps.

b. The Sclerenchymatous Sheath

The sclerenchymatous sheath is an envelope enclosing each meristele. In the marginal parts of the meristele, i. e. in the parts where the sheaths face the gaps, there are may small pores, through which leaf- and root-traces penetrate. There are no other gaps on the sheath.

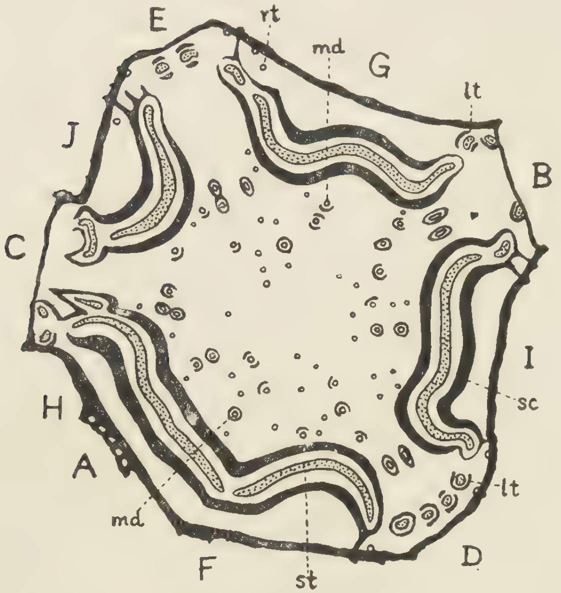


Fig. 22. Transverse section of the stem. (nat. size)

st, stele
sc, sclerenchymatous sheath
lt, leaf-trace
rt, root-trace
md, medullary bundle
A–J, position of leaf-gaps

c. The Leaf–Trace

The number of leaf-traces belonging to a leaf is relatively smaller than in other tree-ferns, there being about thirty in a petiole of the largest size. They are parted from both margins of the gap, and penetrating the cortex enter the petiole, in which they are arranged in a characteristic manner. In the basal part of the petiole, the vascular strands in the periphery are arranged in an elliptical form ; there are also several strands projecting inward from the upper and lateral sides (Fig. 26, A). One pair on the upper side projects deeply inwards, and the pair nearest to the latter, situated at the median upper part, also projects slightly forming with the former an incurved margin. There are two rows of lateral strands, the upper of which consists of two or three pairs and the lower of one pair. The former constitutes with the upper peripheral row of strands the superior series, and the latter with the lower peripheral row the inferior series.

The mode of parting of leaf-traces from the stele is similar to that

in *Cyathea spinulosa*, and they part successively from both margins of the leaf-gap (Figs. 23 & 24). The leaf-gap is fusiform, its broadest part being situated in the upper portion, and the marginal parts on both sides curve outwards considerably. The outward curving of the margin disappears at one place near the broadest part of the gap (Fig. 23, 3), from which part upwards, the curving occurs again, and at last it disappears with the closing of the gap. Leaf-traces parted from the upper side of this constriction of the marginal curvature belong to the superior series, and those from the lower side to the inferior series. The strands of the former series are more closely crowded together than those of the latter. Some traces branch in the cortex or in the petiole. Usually, three or four pairs of traces at the upper arc, exclusive of the deeply projecting pair, are parted as one pair of band-like traces (Fig. 23, 5–6). The deeply projecting pair of the upper arc is the direct continuation of a medullary bundle with no connection to the stelar ring.

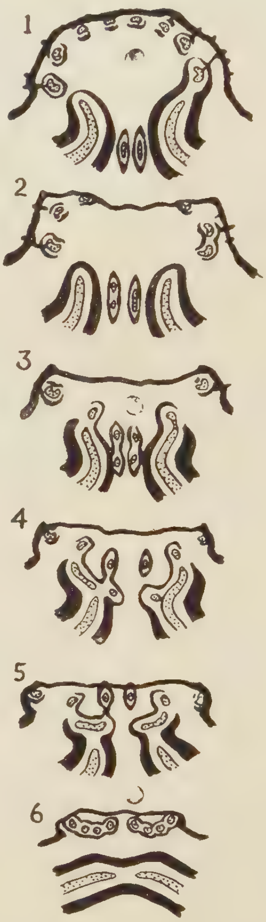


Fig. 23. A series of cross sections through a leaf-gap to show the mode of parting of leaf-traces and the course of the medullary bundles. (nat. size)
Explanations in text.

d. The Root–Trace

Root-traces part from both sides of leaf-gaps, and penetrating the cortex obliquely downwards, leave the stem. The parting portions are limited to the lower half of each gap, and the traces part directly from the stelar margins or from the bases of leaf-traces already parted from the margins.

e. The Medullary Bundle

The number of medullary bundles in a transverse section of a stem is about forty-five, nearly half of which are accompanied by brown sclerenchymatous sheaths. Some sheaths enclose each bundle completely in a continuous ring, but some in an incomplete arc-form.

Though the course of the medullary bundles is not so complicated as in *Cyathea*

spinulosa, yet the tracing of their complete course is difficult, so that only the essential points will be described here.

In each gap there is only a single pair of medullary bundles. Ascending the stem, it passes through the pith to a gap, and penetrating the sheath of the meristele, attaches itself to the latter. Just before this fusion, each bundle bifurcates into two (Fig. 23, 1–3). The dividing part and the course of the branches differ slightly according to the different gaps. Usually, it is where the superior series of leaf-traces is branching that the medullary buudle approaches the margin of the meristele. The bundle fuses with the stele at the curved part somewhat apart from the extreme margin. The fused bundle remains, at first, as a protuberance on the surface of the meristele (Fig. 23, 4). When the bundle penetrates the sheath of the stele, the sheath of the former fuses with that of the latter. The bifurcation of the medullary bundle occurs near this region. In this case, the enclosing sheath of the bundle constricts between the branches, and the outer half surrounds the outer branch completely (Fig. 23, 4–5). The outer branch runs obliquely, and entering the petiole becomes a petiolar strand projecting inward from the upper side. The other branch fuses with the curved part of the meristele in the manner just stated, and the marginal part of the meristele including the part of fusion is parted, in one piece, as a short band or arc (Fig. 23, 5), which is soon divided into three or four leaf-traces (Fig. 23, 6) situated in the median upper part of the petiole. Out of these three or four, the innermost, that is the pair slightly projecting inward at the median part, is derived from the process formed by the fusion of the medullary bundle, that is to say, it is a continuation of one branch of the medullary bundle. Thus, two branches of a medullary bundle proceed upwards to be the median upper and the internally projecting pairs, i. e. the last two pairs of the superior series of petiolar bundles, of which the last pair is the direct continuation of the medullary bundle having no connection with the meristele.

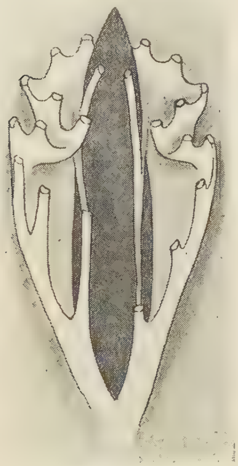


Fig. 24. Reconstruction of a leaf-gap to show the mode of parting of leaf-traces and the course of the medullary bundles.
(nat. size)

The division of the medullary bundle occurs also after it fuses with

the meristele. In this case, the bundle unites with the latter to form a protuberance, the outer part of which is constricted off and runs to the petiole as a leaf-trace.

Tracing the medullary bundles downwards, we find they run through the pith vertically and end blindly, but they are so long and numerous that their whole course cannot be traced with exactness. They often branch or fuse into each other, but they never fuse with the stelar wall itself. The bundles which appear in the pith are small and are not accompanied by sclerenchymatous sheaths. The latter will gradually appear at a part of the stem somewhat higher, and finally enclose each of the bundles completely.

No cortical bundles are found.

Fig. 25. Longitudinal section of the top of a stem. ($\times \frac{4}{5}$)

B. Structure of the Leaf

The size of the leaf differs considerably, the largest measuring 2.5–3.0 meters in length. The petiole is rather long, usually occupying half of the whole length of the leaf. The frond is tripinnate.

a. The Petiole

The petiole occupies nearly half of the leaf-axis and is thicker at the base, gradually tapering toward the rachis.

A cross section of the petiolar base is semicircular in form, the upper side somewhat flattened, and has a transverse diameter of 3 cm. Toward the top the petiole becomes smaller and elliptical in section, and at the upper end of the petiole it reaches 2–1.5 cm. in transverse diameter (Fig. 26). The whole surface is dark glossy purple, and is provided with numerous small processes, especially abundant on the lower side.

Scales often remain on the basal part of the petiole, and are borne on small processes on the surface. On each side of the petiole there is a lineal series of lenticels.

The number and arrangement of vascular strands in the petiole differ in different parts of one and the same petiole and also in different individuals. Now, we shall consider a petiole with the transverse diameter of 2 cm. in its basal part. At the base of the petiole, there are about thirteen pairs of strands showing a characteristic arrangement (Fig. 26, A). Seven pairs of superior strands are arranged in a Γ7–form, of which the upper three or four pairs are almost parallel to the surface of the petiole, the median pair, together with the one situated deeply inward, form the shorter arm of the 7, and the lateral two or three pairs, projecting toward the center, form the longer arm of the 7. The inferior series consists of six or seven pairs, most of which are arranged in an arc parallel to the lower side of the petiole, and a pair on the lateral sides projects somewhat internally. Thus, the superior series is not arranged in an arc at the upper side, but is curved. This latter form is different from the arrangement of the strands in the adult petioles of *Cyathea spinulosa,* but similar to that found in the young petioles of that species. It may be assumed that this type of arrangement is more primitive than that of *Cyathea spinulosa.*

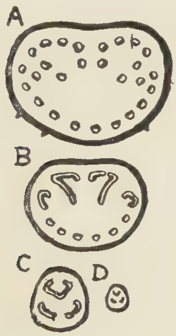


Fig. 26. Transverse sections of four parts of a leaf-axis. (nat. size)

A, Base of the petiole
B, Top of the petiole
C, Middle of the rachis
D, Top of the rachis

The transverse section of each bundle is semicircular at one side slightly flattened, showing a tendency to form a V-shape. Its xylem is V- or U-shape and the orientation is constant in each series respectively. This is due to the mode of constriction of the outward curving of the stelar margins, just as described in *Cyathea spinulosa.*

Tracing the petiolar bundles upwards, we find that the separate strands unite gradually, but this fusion is not accomplished within the petiole. In some cases, at the upper part of the petiole, the superior series is connected to form a pair in a wavy system (Fig. 26, B).

b. The Rachis

The rachis, the continuation of the petiole forming the axis of the frond, tapers toward the end, and on each side pinnae are borne. The

whole surface is dark purple and is covered with fine hairs, especially on the upper side. Vascular strands gradually unite with each other while proceeding upwards. The fusion of strands occurs in the petiole, and becomes prominent within the rachis. Usually, the strands at the superior series unite earlier than those of the inferior. In the first place, the superior series forms two continuous Γ7-formed bands, the longer arms of which soon elongate until both ends fuse into each other, so as to form a V-shaped band (Fig. 26, B–C). Meanwhile, the strands of the inferior series also fuse side by side, but in the median line they are separated, thus forming two auricle-shaped arcs (Fig. 26, C). The formation of these three bands, one upper and two lower, occurs usually at the middle part of the rachis (Fig. 26, C). Each of these bands is of a wavy form. Higher up, the inferior bands are also fused into one. Then, two bands are arranged parallel to each other, finally fusing into one at the very end of the rachis.

c. The Pinna-Axis

A pinna-axis, branching from the rachis, is similar to the upper part of the rachis in its external and internal features. In respect of the vascular system, a few pinna-axes at the basal part of the rachis have four bands. Tracing an axis upwards, we find that two upper strands fuse into a V-shape, and then two lower ones fuse together into a single band.

The mode of branching of the pinna-traces from the rachis-bundles is of the so-called extra-marginal type. On approaching the branching part, the corners of both series of rachis-bundles project, the upper series usually preceding the lower, and the two projecting parts are constricted off, both in the form of a ring. Then, these two rings approach and connect, for a short time, in the form of the figure 8, but soon separate, and are then divided into two to four along the median line.

C. Structure of the Root

Roots, which are adventitious in their origin, cover the stem on all sides, though most of them do not reach the ground. Their length varies greatly. Root-traces part from the lower half of the gap at the marginal part of the meristeles or from the bases of leaf-traces just parted. They run obliquely through the cortex and enter the roots.

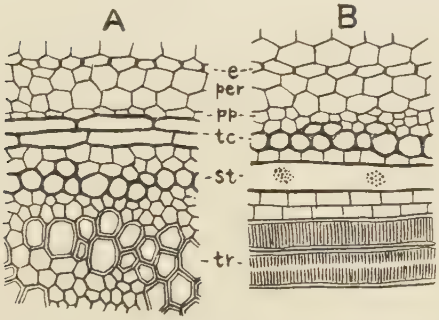
D. Histological Structure of the Stem

a. The Epidermis and the Cortex

The epidermal layer and the outer part of the cortex fall off early. The external part of the stem is covered with a brown sheath, the hypodermal layer. The outer part between the external surface and the stele reaches 6–8 mm. in thickness, of which about 2 mm. belongs to the hypodermal sheath. This sheath consists of two kinds of tissue, the outer thick-walled parenchyma and the inner sclerenchyma. The sclerenchymatous sheath which encloses the meristele is composed of fibers. The cortical part between this sheath and the hypodermis (2–5 mm. in thickness) and that between the sheath and the stele (1–2 mm. in thickness) is of white parenchyma, within which are enclosed numerous longitudinally elongated mucilage sacs. The boundary between the parenchyma and the sclerenchyma is sharply defined, a layer of cubical cells being found between them as a rule.

b. The Stele

The stele of the stem is dictyostelic with an average diameter of 6–7 cm. Each meristele, 1–1.5 mm. in thickness, consists of a normal concentric bundle enclosed in an endodermal layer. The endodermis is distinct showing the characteristic Caspary's points, and encloses the phloem-layer with two or three layers of pericylic cells intervening. The phloem is a relatively thin layer, on the inner side of which are situated one or two layers of sieve-tubes. On the external side, separated from the latter by one or two layers of phloem-parenchyma, there are one or two layers of peculiar cells. In a transverse section they are elongated tangentially, while in a radial section they are almost circular (Fig. 27, tc). They may be called "tangentially elongated cells", or briefly "tangential



Fig, 27. Transverse and longitudinal sections of the phloem-portion of the stem stele. (magnified)

A, Transverse section
B, Longitudinal section
e, endodermis tc, tangential cells
per, pericycle st, sieve-tubes
pp, protophloem tr, tracheids

cells". The presence of such cells was recorded by ZENETTI[1] in the Osmundaceae under the name "Quergestreckte Zellen". On the external side of this layer an irregular layer of the protophloem is present. The xylem is thin, consisting of ten or more layers of scalariform tracheids.

c. The Pith and the Medullary Bundle

The pith is nearly circular. Separated a little from the stelar ring, on the inner side of the latter there is a brown sclerenchymatous sheath, which is the continuation of the same tissue on the outer side of the stelar ring. Exclusive of these sheaths, most of the medullary tissue consists of white parenchyma, within which mucilage sacs, simliar to those in the cortex, are embedded.

A characteristic feature in the pith is the presence of the medullary bundles. They are variable in size, and are almost circular in transverse section, though some of an elliptical outline are seen, especially among those near the gap. A larger bundle accompanies the sclerenchymatous sheath as an arc or a continuous ring. This sheath consists of short fibers corresponding to those on the meristele. The stele of the bundle is of a protostelic type, and is enclosed in an endodermal layer. On the external side of the phloem, a distinct layer of the protophloem is present, but no tangential cells are found. The xylem occupies the central part and consists of a small mass of a few tracheids in a smaller bundle, or of a ring of tracheids with parenchymatous pith in a larger one. In the former case, in the center of the tracheidal mass, and in the latter, in the inner side of the tracheidal ring, there are one or two groups of the smallest tracheids or protoxylems, which show clearly an endarch structure. Even in the largest bundles, no central cavity is found.

d. The Leaf-Gap and the Leaf-Trace

The petiolar base remains for a long while after the foliage has been shed, but falls off afterwards as the effect of the formation of an absciss-layer, or a diaphragm, on the level of the stem surface. The hard peripheral layer and vascular strands of the petiolar base persist for a while.

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1) ZENETTI, P. (1895) Das Leitungssystem im Stamm von Osmunda regalis, L. und dessen Übergang in dem Blattstiel. Bot. Zeit., Jg. 53.

When the leaf-traces parted from the meristele are situated within the stem, they are circular or semicircular in their outline as in the case of the strands in the petiole, but the xylem within the trace consists of tracheids arranged in a V- or U-shape. In the inner corner of the V- or U-shaped xylem, there is a mass of the protoxylem with no cavity in front of it. The phloem encloses the xylem, and in the inner side of the latter, it expands broadly occupying nearly the whole internal groove. Consequently, the endodermal layer does not follow the outline of the internal groove of the xylem, but takes a semicircular or circular shape instead of a V-shape. The central groove of a trace and the accompanying protoxylem appear on the meristelic margin, when the latter is about to part from the meristele as a leaf-trace. The mode of formation of leaf-traces is similar to that in *Cyathea spinulosa*. An internal groove of the xylem at the marginal part of the meristele divides into two, the outer of which becomes the groove of the xylem of the parting trace, and the inner serves in turn as that of the next trace, but bifurcates before parting. In a trace connected with a medullary bundle, the central groove of the xylem is derived from the pith of the latter. In a trace having a direct connection with a medullary bundle, the groove is derived from the pith of the latter, by the opening of the tracheidal ring at one side.

Root-traces parted from the meristele are protostelic, consisting of a large number of tracheids, which diminish gradually, however, until a few remain arranged in a diarch form when they leave the stem. This relation is similar to that in *Cyathea spinulosa*.

E. Histological Structure of the Leaf and the Root

The petiole and rachis are almost the same in their histological structure. The epidermis is a layer consisting of small rectangular cells. Under the epidermis is a layer of the hypodermis, ten or more cells thick. This layer consists of two kinds of tissue, i. e. the outer parenchymatous and the inner fibrous. The walls of both are rather thick and serve as a mechanical tissue; those of the outer part being dark brown, while those of the inner part being almost colourless. Spines on the petiolar surface consist of thick-walled parenchymatous cells. Lenticels on the lateral sides extend into the inner tissue through the hypodermis.

A vascular bundle in the basal part of the petiole is circular or semicircular in transverse section, and has the same structure as that of

the leaf-trace. The xylem shows a V- or U-shape, in the inner corner of which is situated the protoxylem with a large cavity in front of it. This cavity appears after the trace has passed into the petiole. The phloem encloses the xylem on all sides, and expands between the arms of the latter. The protophloem is situated on the periphery of the phloem and is separated by two or three layers of pericyclic cells from the endodermal layer, but between the two arms of the xylem the protophloem is not so distinct. No peculiar tangential cells are found. Outside the endodermis, there is a fibrous layer, which is developed especially on the inner side of the V-shaped bundle.

A wavy strand in the rachis is similar in its essential structure to the separate strands.

Scales found in the younger leaves are of the normal fern-type, and are inserted on the small processes, which are prominent at the basal part of the petiole. Some scales persist for a long time, especially those on the basal part of the petiole. In the rachis, especially on the upper surface, there are filiform multicellular hairs.

The pinnules are of the normal fern-type, and the epidermis consists of wavy cells, with the stomata on the lower side.

The epidermis of the root is lost usually, but dried root-hairs often remain on the surface. The cortex is a thick brown layer consisting of the outer parenchymatous and inner sclerenchymatous tissues. The central cylinder has a diarch xylem.

II. The Young Plant

In order to follow the ontogenetical development of the complex structure of the adult plant, i. e. the size and mutual position of leaf-gaps, the number and arrangement of leaf-traces, the origin and course of medullary bundles etc., young plants were studied. In a young form of this species, the lower tapering conical tip of the stem, which is embedded in the ground, as well as the portion of the stem near the ground, is covered with numerous roots. Serial cross sections of one young plant were made for the study of the solid construction of the stelar system (Fig. 28).

A. Cross Sections of the Stem

Serial sections of a stem for the length of 12 cm. from the lower tip, including forty-one leaf-gaps, were made. The size of the stem as well

as that of the vascular ring differs considerably in different parts of the stem. Therefore, the structure of the stem in cross sections in several regions will now be described.

Region A (the lower tip; diameter 7 mm.; Fig. 28, A). The lowest tip of the stem is usually decayed, and the internal structure is not intact. The region where the structure is preserved is some distance from the very tip, and has a diameter of about 7 mm. A transverse section of this region is of triangular form with rounded corners. The stelar ring is also triangular, its sides being parallel to the stem surface. It has a diameter of 3–4 mm., and in the corners there are three interruptions or leaf-gaps, each of which gives off one pair of leaf-traces. A sclerenchymatous sheath encloses each meristele incompletely. No medullary bundles are found.

Region B (4 mm. from the tip; diameter 11 mm.; Fig. 28, B). The outline of a transverse section of this region is also triangular, and has a diameter of 11 mm. The stelar ring is also triangular with a diameter of 7 mm. In each corner of the latter there is a gap with two pairs of leaf-traces. A sclerenchymatous sheath encloses each meristele completely. Four medullary bundles are found.

Region C (10 mm. from the tip; diameter 13 mm., Fig. 28, C). The outline of the stem in this region is also triangular with a diameter of 13 mm., while the diameter of the stelar ring reaches 8 mm. There are three leaf-gaps in a transverse section, to each of which two or three pairs of leaf-traces belong. The margins of the gap show signs of outward curving. There are seven medullary bundles.

Region D (30 mm. from the tip; diameter 22 mm.; Fig. 28, D). The outline of the stem in this region is an irregular triangle with a diameter of 22 mm. The stelar ring, having a diameter of 15 mm., is divided into three or four segments, the margins of which curve outwards and are characterized by the parting of three or four pairs of leaf-traces. Medullary bundles are twelve in number, those near the gaps being accompanied by sclerenchymatous sheaths.

Region E (60 mm. from the tip; diameter 35 mm.; Fig. 28, E). The outline of this region is triangular with a diameter of 35 mm. The stelar ring, with a diameter of 25 mm., has four leaf-gaps, to each of which four or five pairs of leaf-traces belong. The curving of the stelar margins is very prominent. Medullary bundles reach twenty-one in number, half of which are accompanied by sclerenchymatous sheaths.

Region F (110 mm. from the tip; diameter 40 mm.; Fig. 28, F).

The outline of the stem in this region is an irregular circle about 40 mm. in diameter. The stelar ring, having an average diameter of 26 mm., has five gaps, and five or six pairs of leaf-traces are parted from each of them. The outward curving of the stelar margins and the parting of the last trace in a band-form exhibit the characteristic features of the adult plant. Medullary bundles are twenty-eight in number, most of which are accompanied by sclerenchymatous sheaths.

B. Solid Construction of the Stem

By comparing successive cross sections of the stem, the following points were studied.

a. The Stele

The stele is, broadly speaking, a cylindrical tube broadening upwards, on the wall of which numerous leaf-gaps are present. The diameters of the stem and of the stelar ring in six regions are as follows:

Region	A	B	C	D	E	F
Distance from the tip (mm.)	–	4	10	30	60	110
Diameter of the stem (mm.)	7	11	13	22	35	40
Diameter of the stele (mm.)	3	7	8	15	25	26

The rate of increase of the diameters of the stem and the stele is greatest in the lower part, and diminishes gradually upwards, so that, if we express the increase of the diameter of the stele by a graph, it is represented by a parabolic curve. In this plant, the diagrammatic outline of the stele may be represented by the curve $y^2 = px$, where $p = 15$ (Fig. 28).

b. The Leaf-Gap

In the region A, there are two leaf-gaps. The writer traced upwards as many as forty-one gaps, and was able to ascertain their relative positions and lengths.

The length of the gap increases from below upwards almost in proportion with the stem diameter, as is shown in the following :

Region	A	B	C	D	E	F
Length of the leaf-gap (mm.)	2	4	9	13	15	18

Naturally, the phyllotaxy must accord with the position of the petioles seen externally. In this plant, after the leaves have been shed, the petiolar bases are left on the stem surface, their structure being preserved. The phyllotaxy is not the same throughout the stem, but changes gradually; in the basal part it is nearly $\frac{2}{5}$, but it changes up-

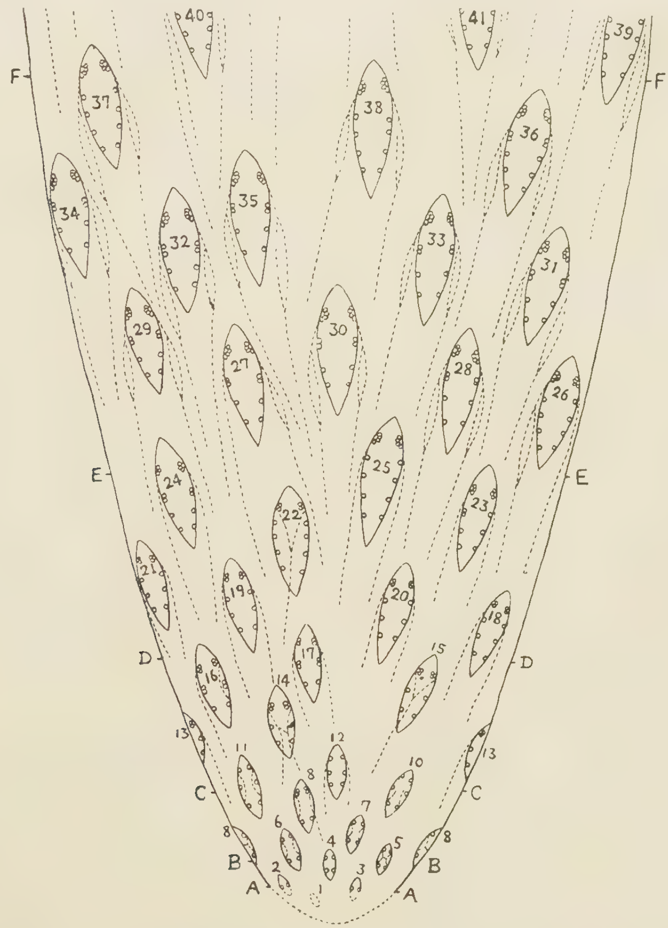

Fig. 28. Developing figure of the stele of a young plant to show the arrangement of leaf-gaps (1–41), the mode of parting of leaf-traces (small circles) and the origin and course of the medullary bundles (dotted lines). A–F show six regions referred to in text. (nat. size)

wards, and near the region E, it becomes midway between $\frac{2}{5}$ and $\frac{3}{8}$, and in the region F, it further approaches $\frac{3}{8}$, or the adult form.

c. The Leaf–Trace

The number and the mode of parting of leaf-traces differ considerably according to the different levels or to the diameter of the stem. As a matter of fact, the leaf-traces at lower levels are less in number and simpler in arrangement, while at the upper part they become numerous, more complex and irregular, as they branch in their course through the cortex. In this way, the number of parting leaf-traces and that of petiolar strands do not coincide, as will be seen in the following table :

Region	A	B	C	D	E	F
Diameter of the petiole (mm.)	2	4	6	10	14	18
Number of leaf-traces (in pairs)	1	2	2–3	3–4	4–5	5–6
Number of petiolar strands (in pairs)	1	2	3	4–5	5–6	7–8

The mode of parting of leaf-traces is almost similar to that in *Cyathea spinulosa*. In a petiole having one pair of traces, the stelar margins at the leaf-gap elongate, and small strands are parted. In a petiole having two pairs of strands, they are parted from the margins in the same manner, and are arranged in the petiole in a circular form, separated from each other by equal intervals. In the case of three or four pairs of traces, the last pair becomes band-shaped by fusion with a medullary bundle, but it is divided into two as soon as it is parted from the meristele, so that in the petiole four or five pairs of strands are present. With five or six pairs of traces, a band-shaped final trace becomes more prominent, and is usually trifurcated after parting, seven or eight pairs of strands thus being present in the petiole. In the latter case, a pair which is the last but one and is parted just above the constriction of the marginal curving, is situated in the petiole somewhat inside the ring of other strands, corresponding to the laterally projecting one of the superior series. The tendency to this lateral projection begins earlier in the 22nd. gap, and gradually becomes prominent, and in the gap with eight or nine pairs of traces, the upper median pair also projects somewhat inwards.

d. The Medullary Bundle

In the basal part of the stem no medullary bundles are found. Somewhat higher up, a few strands appear, and their number increases gradually upwards. Meanwhile, the length of the individual strands increases also, as the following table shows (see also Fig. 28):

Region	A	B	C	D	E	F
Number of the medullary bundle	0	4	7	12	21	28
Length of the medullary bundle (mm.)	—	3	7	15	25	38

The origin and the course of the medullary bundles are somewhat different in different parts of the stem. The first bundle that appears in the pith is the one belonging to the 5th. gap. This gap has two pairs of leaf-traces, and after the parting of the lower pair, the inner side of both meristelic margins thickens internally, and that part is constricted off from the meristele. The parted strand runs through the pith up to the basal part of the second leaf-trace. In other words, in the 5th. gap, a pair of medullary bundles originates as an internal thickening of the meristele and terminates at the basal part of the last pair of leaf-traces in the same gap. In the 6th. and following gaps, there is a pair of medullary bundles. In the 6th. gap, one of the bundles originates as an internal thickening of the stelar ring just as described, while the other appears independently within the pith itself, nearly at the same level as the former. Both strands ascend through the pith and unite with the meristele at the bases of the last pair of leaf-traces. In the 7th. gap, one bundle originates as an internal thickening and the other as an independent formation, and both strands terminate at the bases of the second pair of traces. In the 8th. gap, this relation is similar to the 5th., both bundles originating as the internal thickening of the stelar ring and terminating at the upper part of the gap. The 9th. gap shows both kinds of origin. It must be noted here that, the strand having the independent origin appears below the corresponding gap, so that the former becomes longer than the latter. A pair of medullary bundles belonging to the 10 th. and 11th. gaps originates as the internal projection of the stelar ring. In the 12 th. gap, both bundles arise independently far below the corresponding gap, and terminate at the base of the last pair of traces. In the following gaps, a pair of medullary bundles originates in the pith independently, at a level far below

the bottom of the corresponding gap, and the upper ends fuse with the bases of the last pair of leaf-traces of the same gap, so that the whole length of the strand becomes far longer than that of the gap. At last, the lower end of the strand belonging to a leaf-gap is situated near the lower gap in the same orthostichy. In other words, as the phyllotaxy of this plant is $\frac{2}{5}$ to $\frac{3}{8}$, if we trace a medullary bundle which belongs to a leaf-gap downwards, we find that it continues to the lower sixth to ninth gaps, where it ends blindly. Moreover, as higher in the stem the length of the gap and the mutual intervals between gaps become the greater, so also the length of the individual strands becomes prominent as shown above.

In the lower half of this young plant, the last pair of leaf-traces, which connects with a medullary bundle, is parted in a band-form, which is soon divided into two or three, the innermost of which is the one connected with the medullary bundle. In the upper part of the stem, another change occurs. In the region F, a medullary bundle bifurcates near the bottom of the gap, and the two branches ascend together, but just below the top of the gap, these two fuse into one, which in turn soon fuses with the meristele at the base of the last leaf-trace. The fused part of the stelar margin is parted as a band-shaped trace, which is divided into three. The bifurcation of the medullary bundle begins on one side of the 26th. gap, and in the subsequent gaps it occurs in both bundles regularly. This feature is maintained in the adult plant, though in the latter a medullary bundle bifurcates again before the fusion with the stelar ring, as mentioned above.

The above account describes the normal course of the medullary bundles, but in fact, some irregularities are met with. For example, in some upper parts, there occur two kinds of origin (16th. gap), or a single bundle appears and is bifurcated so as to form a pair (15th. and 22nd. gaps), or a connective strand is present, and connects both bundles in the same gap (5th. and 8th. gaps).

As mentioned above, the course of the medullary bundles is simpler than in *Cyathea spinulosa*, but the occurrence of two kinds of origin is the most important and interesting point in the anatomy of this plant as well as of the Cyatheaceae. In *Cyathea spinulosa*, all of the medullary bundles originate in the pith independently, even in the young stage, while in this species, though most of the bundles show the same origin as in *Cyathea*, there is another mode of origin in the younger stage, that is, the formation by the internal projection of the stelar ring, as in the polycyclic steles found in some Polypodiaceae and Marattiaceae. In

both kinds of origin, the latter type — by internal projection — may be primitive, as it is found in the basal or younger part, so that it may be suggested that the former type — the independent formation — which is the characteristic feature of the Cyatheacean stem, has been derived from the latter type.

Summary

1. The stem of *Alsophila Ogurae* is erect, tapering toward the lower tip and broadening upwards. In the full-grown plant, it reaches a diameter of 6–7 cm., and a height of 2–3 m. The leaves are smaller in the young lower part and larger in the adult upper part. Their bases closely cover all sides of the stem, but older leaves are shed from their bases. Roots, closely grown, in turn cover the stem and leaf-bases.

2. The phyllotaxy is $\frac{2}{5}$ in the younger part, but changes gradually upwards, until it becomes nearly $\frac{3}{8}$ in the adult part. It may be either left- or right-handed.

3. The epidermis and the outer part of the cortex peel off early, and the brown protective sheath, the outer part of which consists of parenchyma and the inner of sclerenchyma, is exposed on the surface of the stem.

4. The stele of the stem is of the dictyostelic type, two or three gaps in a young plant, and five or six gaps in an adult overlapping in a cross section. The margin of the meristele at the leaf-gap curves outwards. Each meristele is enclosed in a brown sclerenchymatous sheath.

5. Histological structure of the meristele is of the normal fern-type, that is, it is constructed in an amphicribral concentric type. The xylem consists of scalariform tracheids and xylem-parenchyma, and the phloem consists of sieve-tubes and phloem-parenchyma, on the outer part of which is a layer of 'tangential cells'. The endodermis is distinct.

6. The sclerenchymatous sheath, which encloses each meristele, is composed of long sclerenchymatous fibers, and in the transitional part between the sheath and the fundamental tissue, there is a layer of cubical cells. In the fundamental tissue there are mucilage sacs, and in the pith there are medullary bundles, of which the larger one is enclosed in a brown sclerenchymatous sheath. The number of the medullary bundles is smaller in the young part, and becomes numerous in the adult, until it reaches more than forty-five in a cross section.

7. Leaf-gaps are small in the young part, and gradually become

larger upwards. They are fusiform, both stelar margins at the gap curving outwards, and from the margins of both sides successive leaf-traces are parted. The curving of the stelar margins disappears or recovers once near the upper part of the gap. Leaf-traces parted from above and below this recovering region belong to the superior and inferior series respectively. This recovering or constriction of the gap-contour begins in the gap with five or six pairs of leaf-traces.

8. The transverse section of a petiole has a circular or elliptical outline. On the surface, which is dark brown, numerous small spines are found. Lenticels are arranged in one row on each side. Scales and fine hairs are abundant in the younger stages, but most of them fall off with the expansion of the foliage. Beneath the epidermis there is a hypodermal layer, and in the fundamental tissue mucilage sacs are embedded.

9. The number and arrangement of vascular strands in the petiole differ considerably in the adult and in the young plants. In the adult, they reach thirty or more in number, most of them being arranged in an elliptical form; also on the upper and lateral sides a few strands are found projecting inward. Marked by this lateral projection, they can be designated as the superior and inferior series. In the younger petiole, the strands are few in number and simpler in arrangement.

10. A cross section of a strand of the petiole is semicircular, and each bundle shows a definite orientation in each series respectively. This is caused by the curving of the stelar margins at the leaf-gap.

11. In the rachis, vascular strands are connected in a wavy form gradually towards the end; in its middle part they make four bands, which are united into three and then into two. Thus, the superior and inferior series are independent throughout the length of the petiole and rachis.

12. Pinna-axes, sprung from the rachis, and second pinna-axes, from the pinna-axis, are similar in their structure to the terminal part of the rachis. In the branching of pinna-traces from the rachis-bundles, the superior and inferior series of the latter continue to the corresponding series of the former, though a small connective strand connects both series in their branching region.

13. The xylem of a petiolar bundle is of an U- or V-shape, in the inner central corner of which there is a protoxylem accompanying a cavity. The cavity is not found in the leaf-trace, but is formed when the trace enters the petiole. The pholem entirely encloses the xylem. The endodermis is distinct, directly enclosed in a thin sclerenchymatous layer.

14. The lamina consists of several layers of assimilating cells, stomata being found only on the lower surface.

15. Root-traces are parted from both sides of the lower half of the leaf-gap. The vascular system of the root is of the normal diarch type, and is enclosed in a thick sclerenchymatous tissue.

16. The medullary bundle is of the protostelic type in its structure, but the larger one encloses a small parenchymatous pith. The endodermis is distinct.

17. A pair of medullary bundles belongs to each gap, and their upper ends fuse with the stelar margin at the bases of the last pair of leaf-traces. Though the bundle bifurcates in its course, two branches are fused again near the end, but a branch is given off near the end and enters the petiole directly. The length of a medullary bundle corresponds to the distance of the neighbouring two gaps belonging to the same orthostichy.

18. Medullary bundles are of two kinds of origin; the one originates as a small internal projection of the stelar ring, which is soon separated in the pith, while the other is formed independently in the pith. The former is found only in the basal or younger part, and may be regarded as a primitive type compared with the latter type of origin.

19. The stele ef *Alsophila Ogurae*, like that of *Cyathea spinulosa*, is a 'Cyathean dictyostele', but its construction is simpler than that of the latter. If we accept the theory of recapitulation, it may be assumed, from the origin and course of the medullary bundles in the younger portions, that the Cyathean dictyostele might have been derived from a kind of the polycylic dictyostelic type and developed in a different direction from the normal polycycly and dictyostely.

IV. Alsophila acaulis, Mak.*

Alsophila acaulis Mak., a fern belonging to the Cyatheaceae, was first described by Mr. T. Makino[1]. One of the important characters of this species consists in its having a creeping rhizome instead of an erect stem. As the name tree-ferns indicates, most of the Cyatheaceae have erect stems, and the creeping habit of this species is a very rare exception. In order to make an anatomical study of this plant, the writer collected material in July 1925, at Yatsuka-mura, Hata-gôri, Kôchi-prefecture, situated 133° E. and 33° N.

The creeping rhizome of the plant lies underground wholly or in part. The leaves, reaching the length of 1.5 m. are borne on the apical portion of the rhizome, so that the plant resembles a Polypodiacean fern. Neverthless, the study of the internal structure of the rhizome and leaves, as well as its sporangial characters has conclusively established its Cyatheacean affinity.

A. External Features and Internal Structure of the Stem

The surface of the stem or creeping rhizome is covered by the bases of petioles and roots. In creeping rhizomes of the Polypodiaceae, the leaves grow upwards and the roots downwards, so that the general appearance is dorsiventral, but the morphological position of their bases are not at all dorsiventral, but radial; the leaves which start from the ventral side of the rhizome turn upwards in process of growth, curving along the lateral side of the rhizome, and the roots do the same[2]. This relative position of the appendages in the Polypodiaceae holds good of this plant also; the leaves and roots are borne radially all around the rhizome in spite of their seemingly dorsiventral habit. A rhizome usually reaches the length of 30 cm., and tapers toward the basal end, i. e. the older part, and its diameter scarcely ever exceeds 3 cm. Living leaves are limited to the top of the rhizome; older ones are shed, leaving

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* The contents of the Part IV appeared in Japanese in the Bot. Mag. Tokyo, Vol. 39, pp. 329–343, Nov. 1925.

1) Makino, T. (1914) Observations on the Flora of Japan. Bot. Mag. Tokyo, Vol. 28, p. 335.

2) Ogura, Y. (1921) On the gaps of the stele in some Polypodiaceae. Bot. Mag. Tokyo, Vol. 35, pp. 113–125.

Fig. 29. Photograph of a rhizome showing its dorsiventral appearance. (× $\frac{1}{3}$)

their basal parts on the rhizome (Fig. 29). The phyllotaxy, judging from the remains of the basal parts of the leaves, is $\frac{2}{5}$ at the base, and is intermediate between $\frac{2}{5}$ and $\frac{3}{8}$ at the top.

a. Cross Sections of the Stem

The structure of the stem in cross section differs somewhat in different parts, but the constructive principle is almost the same, that is, the stem is constructed according to the Cyatheacean type. The stem in cross section is almost triangular, a feature which is due to the attachment of the bases of petioles, and its peripheral part is covered by a thin brown sheath (Fig. 30). The stelar ring runs parallel to the outline of the stem, and is interrupted by two to four gaps, the margins of the meristeles at the gap stretching outwards considerably (Fig. 30, st). The meristele is enclosed in a thin brown sclerenchymatous sheath (Fig. 30, sc). In the pith, some medullary bundles enclosed in sclerenchymatous sheaths are present; usually they are less than ten in number in a cross section (Fig. 30, md). The general aspect of the stem in cross section, therefore, is much like the young stem of other Cyatheacean species, especially that of *Alsophila Ogurae.*

In order to ascertain the solid construction of the stem, serial cross sections of a stem through a length of 130 mm. were made. For this purpose, the writer selected material showing an abnormally constricted part. This was

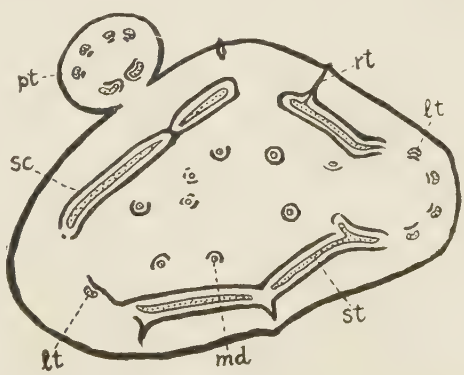

Fig. 30. Transverse section of the rhizome. (× 2)

st, stele
sc, sclerenchymatous sheath
lt, leaf-trace
rt, root-trace
md, medullary bundle
pt, petiole

done in order to see whether the exterally abnormal growth of the stem gives any influence on its internal structure. Descriptions of eight cross sections are as follows.

Region A (near the basal tip; diameter 3 mm.; Fig. 31, A). The tip of the rhizome tapers conically, but the point of the tip is decayed, and the part where the internal structure is preserved has a triangular outline with an average diameter of 3 mm. The stelar ring, with a diameter of 1 mm., has three gaps, from each of which a pair of leaf-traces is parted. No medullary bundles are found.

Region B (8 mm. from the tip; diameter 7 mm.; Fig. 31, B). This part has an irregular triangular outline. The stelar ring is also triangular, and three gaps are found, each with two pairs of leaf-traces. Medullary bundles are not found.

Region C (15 mm. from the tip; diameter 8 mm.; Fig. 31, C). This part is larger than the former, but is similar in structure. In each gap two pairs of leaf-traces are found. No medullary bundles are found.

Region D (30 mm. from the tip; diameter 9 mm.; Fig. 31, D). The gereral structure is similar to the former region, but a single medullary bundle is found.

Region E (48 mm. from the tip; diameter 13 mm.; Fig. 31, E). The stem and stelar ring have a triangular shape, and three gaps are found in the latter, each possessing two pairs of traces, but three pairs of vascular strands are found in the corresponding petiole, as one of the traces bifurcates in the cortex. Six medullary bundles are found.

Region F (the constricted part; 71 mm. from the tip; diameter 10 mm.; Fig. 31, F). This is the part that is slightly constricted, but no essential differences are found in its structure. Two pairs of leaf-traces are found in each leaf-gap, and one of them bifurcates in the cortex. Eight medullary bundles are present.

Region G (98 mm. from the tip; diameter 15 mm.; Fig. 31, G). This region is just above the constricted part. In the stelar ring there are three gaps, in each of which are two or three pairs of leaf-traces. Seven medullary bundles are present.

Region H (136 mm. from the tip; diameter 21 mm.; Fig. 31, H). This part shows a triangular outline with rounded angles. In each of the four gaps, three pairs of leaf-traces are found. Eight medullary bundles are found.

The solid construction of the stelar system was studied by the comparison of these serial sections, as is shown in the following.

b. The Stele

Accompanying the change of the size of the stem, the size of the stelar ring increases from the basal tip toward the top of the rhizome, but in the constricted part of the stem the stele is also constricted as is shown in the following table :

Region	A	B	C	D	E	F	G	H
Distance from the tip (mm.)	–	8	15	30	48	71	98	136
Diameter of the stem (mm.)	3	7	8	9	13	10	15	21
Diameter of the stele (mm.)	1	2	3	4	7	4	8	12

From this table, a diagrammatic development of the stelar surface has been drawn (Fig. 31).

c. The Leaf-Gap

As the petioles parted from the ventral side of the rhizome turn upward, their exact positions of attachment are obscured, and the determination of the phyllotaxy becomes difficult to trace, so that, in order to determine the phyllotaxy, it is better to resort to the position and arrangement of the leaf-gaps. The real arrangement of the gaps is neither influenced by the creeping habit of the stem nor by any abnormal constriction. In the basal part of the stem, the phyllotaxy is nearly $\frac{2}{5}$, and changes gradually toward $\frac{3}{8}$, until in the upper part it becomes intermediate between $\frac{2}{5}$ and $\frac{3}{8}$ (Fig. 31).

The size of gaps varies according to the diameter of the stelar ring, and in the constricted part of the stem the gaps decrease in size as the following table shows (Fig. 31) :

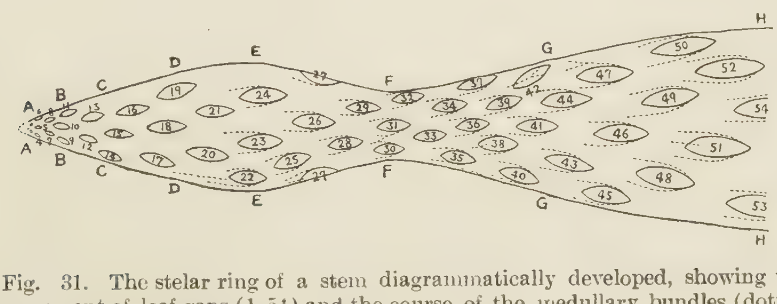

Fig. 31. The stelar ring of a stem diagrammatically developed, showing the arrangement of leaf-gaps (1–54) and the course of the medullary bundles (dotted lines). A–F show the eight regions referred to in text. (× $\frac{4}{5}$)

Region	A	B	C	D	E	F	G	H
Length of the gap (mm.)	3	8	13	20	25	13	20	25

d. The Leaf-Trace

The base of a large leaf, with a diameter of 8 mm., contains six pairs of petiolar strands, of which three pairs of the inferior series are arranged in a semicircular form on the under side, and one lateral pair of three pairs belonging to the superior series projects somewhat inward (Fig. 32). In such a leaf, while three pairs of traces are parted from the stelar margin of the leaf-gap as the inferior series, those of the superior series are parted as two pairs, of which the last bifurcates in the cortex, thus forming three pairs. This relation is maintained also for other gaps in the higher parts, as the following table shows :

Region	A	B	C	D	E	F	G	H
Number of leaf-traces (in pairs)	1	2	2	2	2	2	2	2
Number of petiolar bundles (in pairs)	1	2	2	2	2–3	2–3	3	3–4

e. The Medullary Bundle

The medullary bundle first appears in Region D, and in the regions above there they are always found, but they are not so numerous as in other species of tree-ferns, as is shown in the following table :

Region	A	B	C	D	E	F	G	H
Number of medullary bundles	0	0	0	1	6	8	7	8
Length of the medullary bundle (mm.)	–	–	–	–	20	10	15	25

It is seen from this table that the number of the medullary bundles is less than ten, and that the length decreases at the constricted part of the stem and then again increases gradually upwards.

Though some irregularities are found, the course of the medullary bundles is generally simple throughout the stem. One pair of them belongs to each leaf-gap, and it appears in the pith mostly in the same

level as the bottom of the corresponding gap, and ascending through the pith fuses to the meristelic margins near the top of the gap, the fused parts being parted as the last pair of leaf-traces. The whole length of a bundle, therefore, is nearly equal to the length of the gap.

One of the irregularities in the course of the medullary bundles is that a bundle which appears in the pith ends in it blindly without coming into connection with the stelar ring. Such strands are found several times in different individuals of this plant. In another abnormal case, a strand bifurcates, but both branches fuse again into one before they terminate.

B. Structure of the Leaf and the Root

A leaf reaches a length of 1.5 m., and the petiole occupies nearly all of its lower half. Throughout the petiole and rachis, the surface is dark violet brown. The basal part of the petiole is covered with scaly hairs similar to those found on the stem surface.

The outline of the petiole in cross section is either circular or elliptical, usually with a row of longitudinal grooves on each side, and in each groove are lenticels arranged in a row.

In the basal part of a large petiole, six pairs of vascular strands are arranged as stated before, that is, five pairs are arranged in a circular form, while one lateral pair belonging to the first of the superior series projects inward slightly (Fig. 32, A). In this case, it is rare that two pairs situated at the median upper part are distinguished as two distinct pairs of strands. They are found usually as one pair of band-shaped bundles. In a smaller leaf, the superior strands fuse into a curved pair.

Tracing a larger petiole upwards, separate strands are connected with each other in each series so as to form three or four bands, two superior and one or two inferior (Fig. 32, B). A little further upwards, two superior bands fuse into a V-shaped strand, and the inferior band bifurcates so as to form three bands (Fig. 32, C). The formation of these three bands takes place usually in the middle or upper part of the petiole, but in a smaller leaf

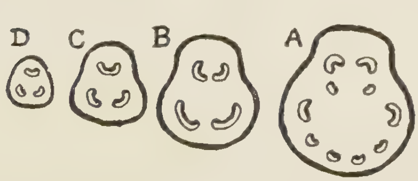

Fig. 32. Transverse sections of four parts of a leaf-axis, showing the arrangement of vascular bundles. (× 2)

A, Base of the petiole
B, Middle of the petiole
C, Top of the petiole
D, Middle of the rachis

it occurs lower down. At the upper part of the rachis, only two strands are found.

The pinna-bundles branched from the rachis are similar in their structure to the upper part of the rachis. The branching of pinna-traces from the rachis-bundles takes place according to the extra-marginal type, viz. they are constricted off from the lateral corners of the superior and inferior strands of the rachis.

Root-traces are parted from the lower and lateral sides of the leaf-gap or from the very bases of the parted leaf-traces.

C. Histological Structure of the Stem

The histological structure of the stem is of the typical Cyatheacean type. In the peripheral region of the stem is a brown hypodermal layer consisting of an outer parenchymatous and an inner sclerenchymatous layer (Fig. 33). The fundamental tissue of the cortex and pith consists of whitish parenchymatous cells, in which numerous mucilage sacs are embedded. The sclerenchymatous sheath of the inner side of the hypodermis as well as that of both sides of the stelar ring is composed of brown sclerenchymatous fibers, and on the boundary between the sheath and the fundamental tissue is a peculiar layer of cubical cells (Fig. 33, cc).

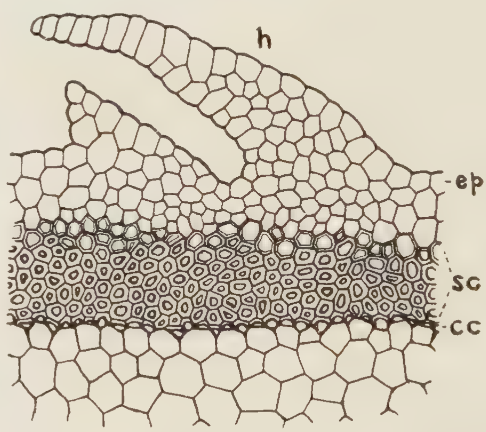

Fig. 33. Transverse section of the peripheral part of the stem. (magnified)
h, hair
e, epidermis
sc, sclerenchymatous sheath
cc, cubical cells

The stele is of a normal 'Cyathean dictyostele'. In each meristele the phloem encloses the xylem, and a layer of tangential cells is found at the external part of the phloem. Most of the medullary bundles are enclosed in sclerenchymatous sheaths. The medullary bundle is protostelic with or without a central parenchyma.

D. Histological Structure of the Leaf and the Root

Notwithstanding the smaller size of the leaf of this species, the structure of the leaf is similar to that of other species of tree-ferns. A

petiolar bundle is semicircular, while its xylem is U-shaped, as the phloem which surrounds the xylem is abundant on the concave side of the xylem, so that an endodermal layer shows a semicircular outline.

The stele of the root, which is enclosed in a thick brown cortex, consists of a diarch radial bundle.

E. The Sporangium

From the middle nerve of a pinnule small branches part on both sides, and on each branch there is a sorus. The sorus, circular in surface view, consists of about twenty sporangia, but lacks an indusium. The sporangium is sessile, ovoid and flattened laterally, and the annulus is somewhat oblique (Fig. 34). Though the dorsal part of the annulus is composed of normal thick-walled cells, about one-third of the ventral side consists of thin-walled stomium-cells. The attaching point of the sporangium is not on the annulose plane, but is on the lateral side, i.e. the annulus occupies an oblique position. The spore is tetrahedral.

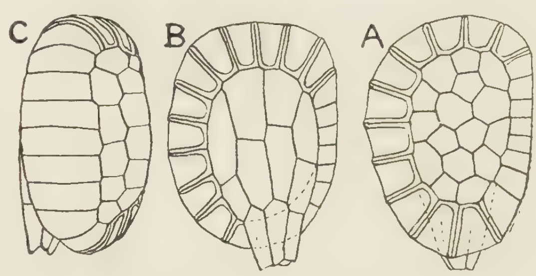

Fig. 34. Sporangia seen from three sides. (magnified)
A, Dorsal view C, Lateral view
B, Ventral view

F. Affinity

Now, let us consider the affinity of this plant based on the facts described above.

a. The Sporangium

The characteristics of the sporangium of the Cyatheaceae are that it has (1) no stalk, except in rare cases, (2) oblique and complete annulus, sometimes containing a small stomium and (3) a transverse rupture.

(1) Stalk. Most of the Cyatheacean sporangia have no stalks, and are borne on small processes or receptacla on the leaf-surface. In some species, short stalks are present as in *Dicksonia*, *Cibotium*, *Alsophila*

pruinata[1]. Most of the Polypodiacean sporangia are characterized by long stalks, although some of them are nearly sessile, e. g. *Dipteris*. The sporangium of the present species is also nearly sessile.

(2) Annulus. The annuli of the Cyatheacean sporangia are complete or include a few stomium-cells. They are always oblique, i. e. the annulus and attaching point are not in the same plane. Those of the Polypodiaceae, on the other hand, are incomplete, i. e. they always contain stomium-cells, and are vertical, i. e. the annulus and the stalk are in the same plane. In both families, some exceptions are known, e. g. *Alsophila blechnoides*[2]; *Loxoma*, *Plagiogyria* and *Cryptogramme*. The annulus of the present species is clearly oblique, the attaching point not being situated in the annulose plane, and is incomplete, one-third of the whole ring forming a stomium. In this respect, the annulus of the present species deviates from the typical Cyatheacean annulus. The writer examined the sporangia of other species of the Cyatheaceae in the material collected by himself as well as in that in the herbarium of our Botanical Institute, but it was found that all of them had incomplete annuli. It may be neccessary, therefore, to change, to a certain extent, the definition of the character of the annuli of the Cyatheaceae, as has been pointed out by some authors[3].

(3) Transverse rupture of sporangium. The transverse rupture of the sporangia is one of the characteristics of the Cyatheaceae and Polypodiaceae, by which these two families can be distinguished from the other related families. The sporangium of the peresent species shows a transverse rupture.

The above characteristics of the sporangia place the present species in the Cyatheaceae.

b. The Sorus

The mode of arrangement of sori on the pinnule in the Cyatheaceae will be classified into two types; the sori situated (1) on the marginal part of the pinnule as in Thyrsopterideae and Dicksonieae, or (2) on the lower surface as in Cyatheeae. In the latter type, there are three forms, (a) with complete indusium — *Cyathea*, (b) with incomplete indusium — *Hemitelia*, and (c) without indusium — *Alsophila*. The

1) Bower, F. O. (1912) Ann. of Bot., Vol. 26.

2) Bower, F. O. (1913) Ann. of Bot., Vol. 27.

3) Atkinson, G. F. (1893) The extent of the annulus, and the function of the different parts of the sporangia of ferns in the dispersion of spores. Bull. Torr. Bot. Cl., Vol. 20.

present species belongs to the last type. But, such a type of sorus is found also in other families such as (a) Gleicheniaceae, which is distinguished from *Alsophila* in having a sorus consisting of a few (usually three to five) sporangia, and (b) some Polypodiaceae, of which a few genera, e. g. *Dryopteris*, are hardly distinguishable from *Alsophila*.

c. The Stem and the Leaf

An important characteristic of this plant is the creeping habit of the stem. In the Polypodiaceae, both forms with creeping and also erect stems are met with, the former predominating. In the stem of the latter, there are two types; (1) with long internodes, usually with creeping rhizomes — *Microlepia, Davallia, Polypodium*, and (2) with short internodes, petioles surrounding the stem so as to give the massive appearance, the stems being either erect — *Metteusia*, or creeping — *Dryopteris*. The Cyatheaceae are characterized by an erect and large stature, as is indicated by the name tree-ferns, although some exceptions are recorded. Descriptions of the ferns are, however, based mostly on the characters of the leaves, so that the characters of the stems are generally unknown. In the case of the Cyatheaceae also, there is no exact statement about the stem. The following species have been described as having small stems not exposed on the ground, but whether they are creeping or erect is not stated, viz. most species of *Balantium*, some species of *Cibotium*, some species of *Dicksonia*, and a few species of *Alsophila*. A creeping stem in this family is rather rare, and in this respect the present species rather approaches the Polypodiaceae.

As the leaf of the present species is rather small like that of the Polypodiaceae, and the essential points in the external characters of the leaf resemble each other in the Polypodiaceae and Cyatheaceae, we cannot, by the external characters, distinguish to which of the two families the present species belongs.

The cross sections of the stem and the leaf, however, are of the characteristic Cyatheacean type, and at once distinguish the species from the Polypodiaceae.

d. Conclusion

The general features of the stem and leaves, the form and arrangement of the sori of the present species are rather like the Polypodiaceae, but the anatomical structure of the vegetative organs as well

as the structure of the sporangia are decidedly of the Cyatheacean type, so that this species should be included in *Alsophila* as has been done by Mr. Makino.

One point needing discussion is the creeping habit of the stem. As above mentioned, the exact character of the stem of *Alsophila* is not given. The species of *Alsophila* known as possessing a creeping rhizome is *Al. blechnoides*, Hk., but the structure of the vegetative organs and sporangia of this plant is not typically Cyatheacean as was shown by Bower (1913), and it has been included in another genus *Metaxyla* (*M. rostrata*, Pr.). *Al. Sprucei* is also described as possessing a creeping rhizome, but this has not been confirmed. So far as the known species of the true *Alsophila* are concerned, there is none in which the creeping habit has yet been established, and it may be considered that *Al. acaulis* is the only species which has the creeping habit. It may be mentioned that the writer has observed several times that the young stems of other tree-ferns creep before they grow and become erect. Moreover, it is believed that the erect habit of the fern-stem is derived secondarily from the primary creeping habit[1]. Therefore, it must be considered whether the creeping habit of this plant is due to the climatic condition of the habitat or to the genetical character of the plant itself. The locality where this plant grows — Yatsuka-mura, 33° N. — is the northern limit of the habitat of the Cyatheaceae in Japan, and lies almost in the same latitude as other places, where *Cyathea spinulosa* grows as high as 3 meters, viz. Hachijô Island, 32° 40′ N. and the Gotô Islands, 32° 40′ N. Therefore, the place where *Al. acaulis* is growing now has all conditions, in which Cyatheacean species can actually grow up to the tree-form, and the writer is inclined to the opinion that the creeping habit is the normal character of this plant.

Summary

1. The stem of *Alsophila acaulis* is a creeping rhizome, either subterranean or above ground. It tapers toward the end and thickens toward the top, and is about 30 cm. in length and 3 cm. in diameter. The leaves are borne radially around the stem, and the older leaves fall off from their petiolar bases leaving scars on the stem. In general features, the stem and leaves resemble those of some of the Polypodiaceae.

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1) Bower, F. O. (1913) Ann. of Bot., Vol. 27, p. 453; —— (1908) Origin of Land Flora, p. 626; —— (1923) The Ferns. Vol. 1, p, 32.

2. In cross section, the stem is nearly triangular influenced by the petiolar bases. In the peripheral region of the stem there is a brown layer, the outer half of which is composed of parenchyma and the inner half of sclerenchyma. From some parts of the epidermis arise scaly hairs which cover the stem surface. The fundamental tissue consists of whitish parenchyma, in which some mucilage sacs are embedded.

3. The stelar ring is triangular in cross section and nearly parallel to the stem surface. The stele is a dictyostele, interrupted by from three to five gaps in a cross section. The margins of meristeles elongate outwards and part the leaf-traces successively. Each meristele consists of a normal concentric bundle, and on the periphery of the phloem is a layer of tangential cells.

4. Surrounding each meristele is a characteristic brown sclerenchymatous sheath composed of sclerenchymatous fibers. This sheath is separated from the fundamental tissue by a layer of cubical cells.

5. The pith occupies the central part of the stem and consists of parenchyma, in which mucilage sacs and medullary bundles are found. The lattter can be readily recognised as they are enclosed in brown sclerenchymatous sheaths. The medullary bundle itself is protostelic.

6. The phyllotaxy is not influenced by the creeping habit of the stem, and maintains a radial arrangement. It is $\frac{2}{5}$ in the basal part, but changes gradually toward the top, until at the summit it becomes intermediate between $\frac{2}{5}$ and $\frac{3}{8}$.

7. The medullary bundles are not found in the basal part of the stem, but appear in the upper part. They are less than ten in a cross section, and a pair of them belongs to each leaf-gap. One pair appears in the pith near the basal part of a leaf-gap, and ascending through the pith unites with the meristelic margins at the upper part of the gap. The fused parts of the meristeles are parted and form the last pair of leaf-traces in the gap. Some bundles take an irregular course, and end blindly in the pith.

8. The leaf-traces are parted from both margins of the gap. There is only one pair in the smaller gap at the basal part of the stem, but they increase upwards until there are three or four pairs in the larger upper part. Some of them branch in the cortex of the stem, so that the number of vascular strands in the petiole is larger than that of the traces parted.

9. A constricted part of the stem shows a reduction of the size of the gaps and of the length of the medullary bundles, but does not affect

the arrangement of the leaf-gaps, the number and course of the medullary bundles and the mode of parting of the leaf-traces.

10. The surface of the petiole and rachis is dark violet brown, and the basal part of a large petiole measures 8 mm. in diameter. Beneath the superficial parenchymatous layer is a hypodermal layer composed of sclerenchymatous fibers. In the fundamental tissue mucilage sacs are embedded.

11. In the base of a large petiole there are six pairs of strands, of which every three pairs are classified as superior and inferior strands. Of these pairs, one lateral pair corresponding to the first pair of superior strands turns a little inwards. Tracing the petiole upwards, the superior strands unite in a V-shaped arc, and the inferior ones into two bands, which then fuse into one strand. The mode of branching of pinna-traces is of the so-called extra-marginal type.

12. A petiolar bundle consists of the central xylem enclosed by the phloem. The latter fills up the inner groove of the former, so that the endodermal layer shows a semicircular outline. Close to the protoxylem, at the inner corner of the xylem, is a cavity.

13. The root-traces are parted from the basal and lateral parts of the leaf-gaps, and penerate the cortex obliquely downwards. A root has a diarch bundle enclosed in a thick cortex.

14. The sori, lacking indusia, are borne on nerves on the lower surface of the pinnules. Each sorus is circular and composed of about twenty sporangia. Each sporangium is nearly sessile, has oblique annulus, and is incomplete including some stomium-cells.

15. The shape of the stem and leaves as well as the shape and arrangement of the sori of *Alsophila acaulis* are of the form that is rather familiar in the Polypodiacean species, but the internal structure of the vegetative organs and the construction of the sporangia clearly indicate its Cyatheacean affinity, and justifies the classification of this species in the genus *Alsophila*.

16. Of the species of *Alsophila* with creeping rhizomes this species shows this character most distinctly.

V. Alsophila Bongardiana, Mett.*

Alsophila Bongardiana is a tree-fern, endemic to, and very common in the Bonin Islands. The material was collected in January 1925, on Chichi-jima (Father Island).

I. The Adult Plant

In old individuals, the stem is straight and tall, attaining a height of 10 meters or more. It bears at the apex a rosette of leaves. The leaves, when dead, fall off leaving on the stem surface prominent leaf-scars studded with vascular strands in a peculiar arrangement. Occasionally, especially in young or small plants, the stem is invested with scaly hairs. In older portions of the stem, these appendages generally disappear, and frequently lichens and mosses are found growing on the stem surface.

A. The External Features of the Stem and the Phyllotaxy

In tree-ferns the stem varies considerably in external appearance and thickness at different heights. In studying this point, *Alsophila Bongardiana* furnishes good material, because of its having the surface of the stem nearly all exposed. Moreover, the distinct leaf-scars make easy the determination of the leaf-arrangement. On this account, the following four different parts of a stem, about 5 meters in height, were subjected to examination.

Part I (about 1.5 m. above the ground ; diameter 138 mm.; Fig. 35, left). This part represents the lower part of the stem, and is conical, measuring 138 mm. in diameter. The surface of the stem is smooth. The leaf-scar assumes a long elliptical shape, the longer or vertical axis being 95 mm., and the shorter or horizontal one 33 mm. in length. In a leaf-scar upon the surface of the stem, vascular strands, about 70 in number, are visible in regular arrangement. Most of the strands are arranged in a ring along the margin of the scar, and in addition to these, there are a series of strands within the ring (Fig. 39). Leaf-scars are arranged on the stem, widely separated from one another. Their

* The contents of the Part V appeared in Japanese in February number of the Bot. Mag. Tokyo, Vol. 40, pp. 69–90, 1926.

arrangement is not exactly $\frac{3}{8}$, but deviates slightly toward $\frac{2}{5}$, that is, the 9th. scar is situated not exactly above the first, but a little forward across the vertical row of the latter. The interspace between any two scars in a vertical row, though it is not strictly vertical, is about 215 mm., or more than twice the long axis of the scar. The remains of adventitious roots constitute another characteristic feature of the stem surface. Just below the scar, they occupy, on the stem surface, an area of a long stalactic shape, attaining about 180 mm. in length. As root-traces part from the lower half of the leaf-gap, the area occupied by roots shows precisely the position of the leaf-gap. In a cross section of this part, there is a stelar ring interrupted by six or seven leaf-gaps, which are not situated at equal distances, as the phyllotaxy is not precisely $\frac{3}{8}$ (Fig. 42, left).

Part II (about 2.5 m. above the ground ; diameter 120 mm. ; Fig. 1, right). This is a cylindrical part with a diameter a little smaller than

Fig. 35. Photograph of two parts of a stem showing the form and arrangement of leaf-scars. ($\times\frac{1}{5}$)
Left, Part I; white patches are lichens Right, Part II

the former. The long axis of the leaf-scar is much shorter than the former part, measuring 48 mm., while the horizontal short axis measures 39 mm. The arrangement of about sixty vascular strands on the scar is quite similar to that in the former case. The scars, lying more closely than in the former part, show a $\frac{3}{8}$ arrangement. The interspace left between any two scars in a vertical row is as small as 45 mm. The spaces on the stem occupied by the roots, which are of stalactic form, approach one another closely, leaving almost no free surface between

them. Moreover, some of the roots cover the surface of the scars. Owing to the $\frac{3}{8}$ phyllotaxy, the stelar ring in cross section appears to be cut into eight equal segments.

Part III (about 4 m. above the ground ; diameter 120 mm.; Fig. 36, right). Though this part has a thickness similar to that of Part II, the external features of the stem differ considerably. Leaf-scars lie close

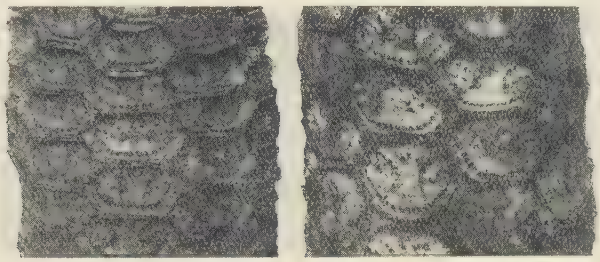

Fig. 36. Photograph of two parts at higher levels of the stem shown in Fig. 35, showing crowded leaf-scars. ($\times \frac{1}{8}$)

Right, Part III　　Left, Part IV

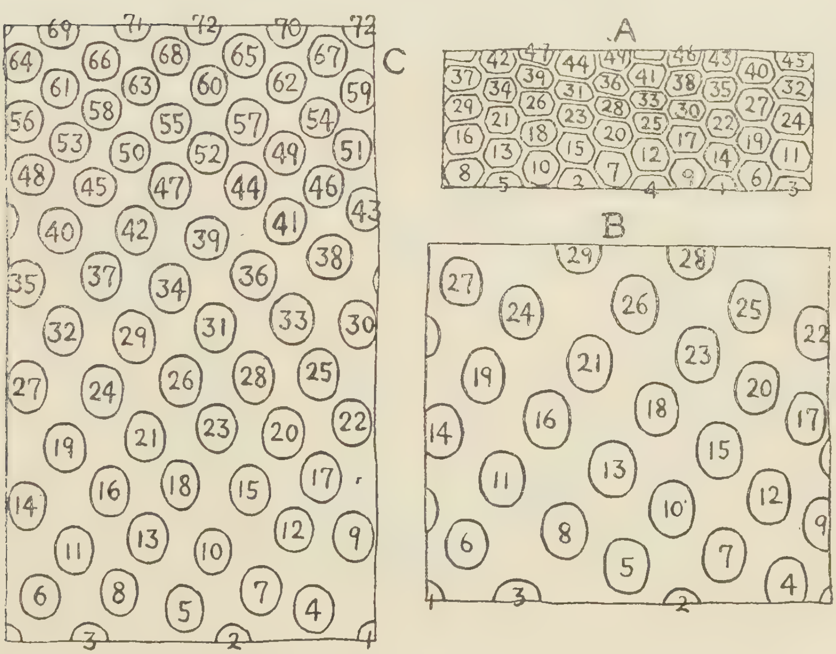

Fig. 37. Diagrammatic figures of the stem surface at different parts to show the change of arrangement of leaf-scars. ($\times \frac{1}{7}$)

A, Part III　　B, Part II

C, Transitional part from A-type to B-type

together leaving only narrow interspaces between them. Each scar has an elliptical shape with a horizontal axis of 48 mm. and a vertical axis of 30 mm. The vascular strands in each scar are arranged in the same manner as in Parts I and II. The leaf-scars are arranged in vertical rows, the arrangement of scars in adjacent rows being somewhat discrepant from each other. In some parts where the scars are crowded together, they take an hexagonal shape from compression. The interspace between the scars, that is the stem surface proper, is very narrow and is usually covered with scales. No roots are visible. The phyllotaxy of this part seems to be represented by a regular radial type of $\frac{3}{10}$ or some such formula, but in reality, it is different. In detail, five scars on every five other vertical rows are situated nearly at the same level (Fig. 37, A, 1 2 3 4 5, 11 12 13 14 15, . . .), and five scars on another five rows are also at the same level (6 7 8 9 10, 16 17 18 19 20, . . .), so that it seems as if the scars were arranged in two series of a five-whorled type, but this again is not so. The origin of this mode of arrangement can be assumed from an examination of the transitional part between this and the former Part II. In this transitional part, it can be found that this type of arrangement in Part III may be derived from the $\frac{3}{8}$ type, in an irregular manner, as shown in the figure (Fig. 37, C). In a cross section of this part, the stelar ring is segmented into ten meristeles, each curving in a semicircular form, and it is found that the gaps of every other five rows are nearly in the same structure (Fig. 42, right).

Part IV (about 5 m. above the ground ; diameter 110 mm., Fig. 36, left). This part has a cylindrical shape with a thickness a little smaller than in the former part. The compression of the internodes and the close contact of the scars become severe, and consequently the scars are pressed on one another so as to become nearly hexagonal, leaving no interspaces between them. Each scar flattens vertically, measuring 19 and 40 mm. in vertical and horizontal diameters respectively. The scars are arranged in regular vertical rows as in Part III, but the rows are eleven instead of ten, so that in a cross section of this part, the stelar ring is divided into eleven equal parts This type of arrangement is derived from the former in an irregular way.

B. Cross Section of the Stem

The stem shows the typical Cyatheacean form in cross section, being characterized by the occurrence of numerous medullary and some cortical bundles.

In the first place, the structure of a stem, 110 mm. in diameter, will be given. In general features and the arrangement of left-scars, this material is similar to Part II above referred to. Each scar is circular in form, with a diameter of 40 mm., and the arrangement of the scars shows a type intermediate between $\frac{2}{5}$ and $\frac{3}{8}$. The outline of the stem in cross section is nearly circular, though with some irregularities at the leaf-gap (Fig. 38). The stelar ring, with a diameter of 95 mm., lies nearly parallel to the stem outline, and is segmented by five or six leaf-gaps. From the position of the leaf-gaps its phyllotaxy can be estimated as intermediate between $\frac{2}{5}$ and $\frac{3}{8}$ (Fig. 38, A—J). On both sides of the stelar ring is the sclerenchymatous sheath with a thickness of about 3 mm. (Fig. 38, sc). The margins of meristeles bordering the leaf-gap curve outwards, and leaf-traces are parted from the margins

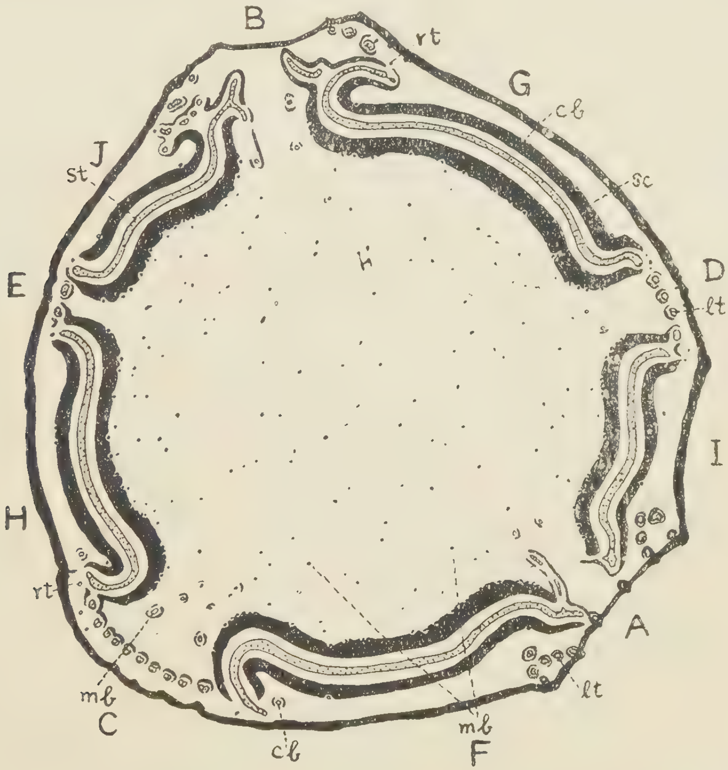

Fig. 38. Cross section of the stem. ($\times\frac{4}{5}$)

A—J, position of leaf-gaps
st, stele
sc, sclerenchymatous sheath
lt, leaf-trace
rt, root-trace
mb, medullary bundle
cb, cortical bundle

(Fig. 38, lt). The pith, which is enclosed in the inner sclerenchymatous sheath of the stelar ring, occupies the greater part of the stem, and is rendered prominent by the existence of a greater number of medullary bundles (Fig. 38, mb). They reach about 240 in number, but the majority of them are liable to be overlooked, as they are not accompanied by sclerenchymatous sheaths. They are more numerous in the peripheral region of the pith than in the central region, and when they come in contact with the sclerenchymatous sheaths of the stele, small grooves are formed in the latter, in which the bundles are buried. The size of these grooves varies, and occasionally two bundles are found within a single groove. In these cases, the position of the bundles is easily recognized. In some rare cases, a medullary bundle is enclosed completely within the sheath. Several bundles near the leaf-gaps are somewhat larger than the others, and have brown sclerenchymatous masses. Occasionally, bundles other than those near the leaf-gaps have brown sheaths.

One of the peculiar characters of this species is the presence of the cortical bundles, which are situated in the cortex in contact with the outer surface of the sclerenchymatous sheath (Fig. 38, cb). They are few in number; 15–20 in cross section, that is 2–3 for each meristele. Most of them are in contact with the sclerenchymatous sheath of the stele, forming small grooves on the outer surface of the latter, just as the medullary bundles do on the inner surface of the same sheath of the pith. The cortical bundles near the leaf-gap, however, are surrounded by thick brown sclerenchymatous ring.

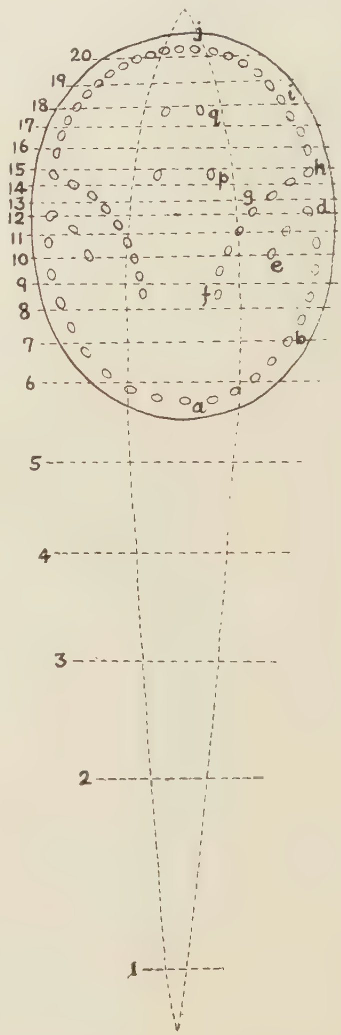

Fig. 39. A leaf-scar showing the arrangement of vascular strands and the position of the leaf-gap. Dotted lines show the outline of the gap; parallel lines correspond to the parts of cross sections of Fig. 40; the lettering of leaf-traces refers to those of the same figure. (nat. size)

C. Solid Construction of the Stem

By a combination of serial corss sections of the stem above referred to, its solid construction, especially of the stelar system, was studied.

Fig. 40. A series of consecutive cross sections through a leaf-gap, showing the mode of parting of leaf-traces and the course of the medullary and cortical bundles. Sections in this figure correspond to the levels shown in Fig. 39, and the leaf-traces denoted by letters correspond to those shown in the same figure. (nat. size)

Other explanations in text.

a. The Stele

The stele is a hollow cylindrical tube with a diameter of 8–9 cm., and its wall is perforated by numerous fusiform leaf-gaps, which are arranged according to a type intermediate between $\frac{2}{5}$ and $\frac{3}{8}$.

b. The Leaf–Gap and the Leaf–Trace

The vertical length of a leaf-gap reaches about 100–120 mm., which is three times that of the leaf-scar (Fig. 39). The broadest part, measuring about 10–15 mm., is not in the middle, but somewhat above it. The outward curving of the stelar margins at the gap is so remarkable in this plant that the curved marginal part becomes nearly parallel to the main body of the stelar ring (Fig. 38, B C). The marginal curving is not simple, and in the upper part there is a portion where the curving disappears, so that the curved margin on each side consists of two parts (Fig. 41). Leaf-traces parted from the upper and lower parts of this recovering portion of the curving belong to the superior and inferior series respectively.

The mode of parting of leaf-traces is almost the same as in *Cyathea spinulosa*, but as their number is large in this species, this mode is more complex than that in *Cyathea* (Figs. 39–41). Let us now trace a gap from the bottom upwards. At first, the stelar margins of the gap turn out, parting the leaf-traces consecutively (Fig. 40, 1–4, a–b). In a cross section at the lower part of the scar, six or seven pairs of traces are arranged in an arc between the two stelar margins (Figs. 39 & 40, 5–6). Inside the entrance of the gap, a number of pairs of medullary bundles are arranged in two rows, the first pair being about to fuse with the meristele. At a little level above, this pair of the medullary bundles penetrates the sclerenchymatous sheath, and fuses with the stelar surface (Fig. 40, 6–7). After this fusion, the bundle remains on the stelar surface as a process at the entrance of the gap (Fig. 40, 6–7). At a slightly higher level, the original curved margin of the meristele is separated, as a whole, from the stele (Fig. 40, 7–8), so that the process formed by the fusion of the medullary bundle becomes the very margin of the meristele, which turns toward the median line of the gap (Fig. 40, 8–9). This corresponds to the part where the outward curving of the stelar margin disappears. The separated band-formed bundle is divided into strands, usually four in number, which become leaf-traces corresponding to the lateral projection of the inferior series (Fig. 40, 8–11, d–e). At the same time, the marginal portion of the newly formed

stelar margin gives off leaf-traces, which belong to the lateral projection of the superior series (Figs. 39 & 40, 8–10, f–g). Meanwhile, this new margin begins to turn outwards (Fig. 40, 10–11), and the following two or three pairs of medullary bundles fuse with the inner surface of the meristele in this region (Fig. 40, 8–11). This fusion is complete, so that no processes are formed on the stelar surface. Higher up, a cortical bundle approaches the curved stelar margin (Fig. 40, 11, c), and finally fuses with it, thus making the marginal turning of the meristele very prominent (Fig. 40, 12). Then, the margin thus formed gives off a leaf-trace which is situated at the lateral corner of the superior series (Fig. 40, 13, h). From the stelar margin, hereafter, there are parted consecutive leaf-traces, which are situated on the upper side of the scar (Fig. 40, 14–18, h–i), and with some of these, a few medullary bundles are connected. Meanwhile, the gap becomes narrower, and at the same time, the outward curving of the meristele becomes less prominent (Fig. 40, 17–18). It is on the inner surface of the curved part of the meristele near its very margin, that the last medullary bundle connects with the meristele (Fig. 40, 15–16). The last bundle remains on the stelar surface as a process, giving a forked appearance to the stelar margin (Fig. 40, 17). The forked marginal part is separated from the main stelar part as a single piece, and then is divided into a number of strands, which are the leaf-traces at the median upper part of the scar (Fig. 40, 17–20, i–j). Thus, the process of the parting of the leaf-traces is accomplished, and the gap is closed a little higher up. Some branches of the medullary bundles, however, go directly to the petiole, and give rise to the isolated leaf-traces on the inside of the upper arc (Fig. 40, 14–18, p–q).

c. The Medullary Bundle

The course of the medullary bundles of this species is very complicated, as they are numerous and connect with each other forming a complex network. Indeed, if a bundle is traced upwards or downwads, it connects with other bundles, or bifurcates into two, which again fuse with each other or with another bundle, or again branches. The strands, therefore, are connected with one another in so complex a manner that it is quite impossible to trace them exactly. Such a condition is not peculiar to this species, being common to all Cyatheacean medullary bundles, but in the present case, it is far more complex than in other species. In extreme cases, the bundles run in oblique or transverse directions. They take, however, a definite course in terminating, the

lower ends appearing in the pith and the upper ends connecting with the stelar margins at the leaf-gap.

The medullary bundles that have the connection with a leaf-gap are not constant in number, as they separate or fuse with one another, even within the gap. There are usually more than five or six, but less than ten, pairs of them. Their course at the gap is not all the same, but differs even on different sides of one and the same gap. Therefore, a case of usual occurrence will now be considered (Figs. 40 & 41).

Tracing a leaf-gap from below upwards, at the level where the gap appears for the first time, no medullary bundles belonging to the gap are found (Fig. 40, 1–2). It is at the level where two or three pairs of leaf-traces are parted that the medullary bundles become visible; they are arranged in two rows within the gap, and moreover, are prominent accompanied by brown sclerenchymatous sheaths (Fig. 40, 3–4). At the level where some leaf-traces are parted, five medullary bundles accompanied by brown sclerenchyma are arranged in a row at one side of the entrance of the gap (Fig. 40, 5). Higher up, the first two fuse into a single strand, which penetrates the sclerenchymatous sheath of the stele and fuses into the stele with one end, while another end projects toward the gap, giving a forked appearance to the stelar margin (Fig. 40, 6–7). The new inner margin thus formed is then cut off as a leaf-trace situated at the innermost part of the lateral projection of the superior strands (Fig. 40, 8–9, f). Therefore, the first leaf-trace of the superior series may be considered to be the continuation of the first medullary bundle. Meanwhile, the outer or original margin is separated from the main stele, as one piece, which divides into some leaf-traces belonging to the inferior series (Fig. 40, 9–11). Then, the third medullary bundle fuses with the incurved part of the meristele, the fused part being separated as the second superior leaf-trace (Fig. 40, 8–9). Next, the fourth and fifth bundles consecutively fuse with the meristele near its margin, and these parts give rise to the third and fourth superior leaf-traces. Prior to this, the sixth bundle has appeared on the inner side of the fifth, and bifurcated. One of its branches bifurcates again, and thus three strands are formed, one of which branches again so as to form a fourth, but two of these fuse together, and then another bundle bifurcates. Thus, four branches of medullary bundles, sixth to ninth, are formed. The sixth bundle fuses with the stelar margin in usual manner, and that fused part produces the seventh leaf-trace situated near the outer corner of the laterally projecting series. Meanwhile, a cortical bundle approaches the curved stelar margin and fuses with it,

thus making the outward curving of the stelar margin very remarkable (Fig. 40, 11–12). Then, the seventh medullary bundle fuses with the inner surface of the curved margin, and gives rise to a leaf-trace situated on the upper side of the scar. The eighth bundle proceeds directly outwards though the gap, without connecting with the stele, and becomes an isolated leaf-trace situated under the upper arc of series of strands (Fig. 40, 14, p). The ninth or last bundle ascends to the upper part of the gap, and connects with the meristele with one end (Fig. 40, 15–16). In this case, the curved part of the stelar margin becomes less prominent by the parting of consecutive leaf-traces, and the connection of the last medullary bundle produces a forked margin (Fig. 40, 17). The forked part, as a whole, is separated from the main stele, and is then divided into several strands or leaf-traces situated on the median upper side of the scar (Fig. 40, 18–19, i–j). In this case, prior to the fusion of the last medullary bundle with the meristele, a branch is given off, which, entering the petiole directly through the gap, becomes an isolated leaf-trace above the isolated one derived from the eighth medullary bundle (Fig. 40, 18, q).

The above description gives about the course of medullary bundles on one side of any one gap, while in other gaps their course is somewhat different. The important point of difference lies in the number of the branches of the medullary bundles. Briefly speaking, some pairs of medullary bundles are arranged in two rows within the gap. Their upper ends finally fuse with some parts of the stelar margin at the leaf-gap, the fused parts being separated as leaf-traces belonging to the superior series; the first bundle gives rise to the first leaf-trace, the last to the last, and the intermediate bundles to the intermediate traces, while some branches of the few last bundles enter the leaf directly through the gap, and form isolated traces situated to the upper part. The branching of the isolated strands occurs at different levels, and when it occurs near the very end of the main bundle its origin is very clear, but this is not always the case.

d. The Cortical Bundle

The presence of cortical bundles is one of the structural characters of this species. A pair of them belongs to each leaf-gap. Their course is very simple compared with that of the medullary bundles. They appear in the cortex independently, and ascend vertically along the outer surface of the sclerenchymatous sheath of the stele. Tracing a bundle upwards. it becomes distinct as it aquires a sclerenchymatous

sheath (Fig. 40, 2, c), and becomes more and more prominent with the thickening of the sheath (Fig. 40, 3–5). Gradually it approaches the curved margin of the meristele at the gap, and finally fuses with the margin (Fig. 40, 5–6). But, this fusion is temporary, for the cortical bundle soon separates from the stelar margin (Fig. 40, 7–8), and ascends a little enclosed completely again in the sclerenchymatous sheath (Fig. 40, 9–11). The stelar margin, to which the cortical bundle has fused, is separated as a leaf-trace situated at the lateral corner of the inferior series. Meanwhile, the outward curving of the stelar margin disappears owing to the fusion of the first medullary bundle, and then the new margin thus formed again curves outwards. It is in the region where the curving becomes extreme that the cortical bundle connects with the meristele (Fig. 40, 12). This fusion makes the curving of the stelar margin very prominent. The margin thus formed is soon separated as a leaf-trace situated at the lateral corner of the superior series (Fig. 40, h). This trace, therefore, is derived from the part combined with the cortical bundle.

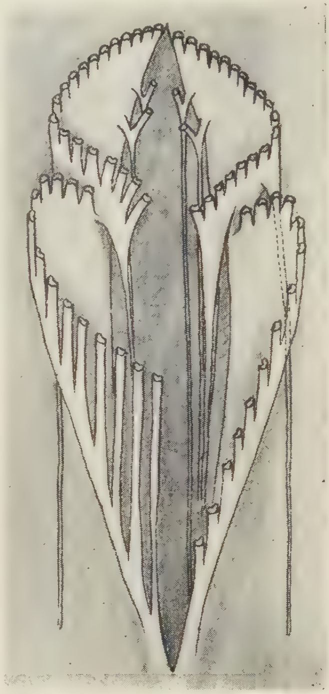

Fig. 41. Reconstruction of a leaf-gap, showing the mode of parting of the leaf-traces and the course of the medullary and cortical bundles. (nat. size)

Tracing a cortical bundle downwards it gradually leaves the stelar margin, and approaching the outer surface of the sclerenchymatous sheath of the stele, comes in contact with it, making finally a groove on the surface of the sheath. Then, the bundle becomes smaller, and finally ends blindly, and, at the same time, the groove of the sheath disappears. The whole length of a cortical bundle is not constant, but it seems to be as long as twice that of the gap to which the bundle belongs.

In short, the pair of cortical bundles belonging to a gap appears in the cortex far below the gap, and ascending through the cortex fuses with the curved margin of the meristele, and gives rise to a pair of leaf-traces situated at the lateral corners of the superior series. But, before the fusion, the bundle usually connects temporarily with a leaf-trace belonging to the inferior series.

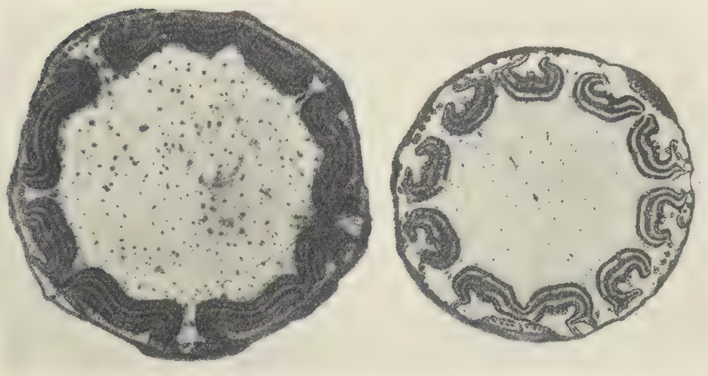

Fig. 42. Photograph of cross sections of two parts of the stem shown in Figs. 35 and 36. (× ⅓)

Left, Part I Right, Part III

Fig. 43. Cross section of a higher part (Part III) of the stem with leaf-scars arranged in ten vertical rows. (× ⅘)

Abbreviations as in Fig. 38.

e. The Case of a Stem with Crowded Leaves

The higher part of the stem shows crowded leaf-scars as before mentioned. To ascertain whether the internal structure in such a part differs from that of Part I above described or not, the writer examined material of Part III, that is the part with scars arranged in ten vertical rows.

In a cross section of this part, with a diameter of 120 mm., the stelar ring is divided into ten meristeles, each of a semicircular shape (Figs. 42 right and 43). Therefore, the form of the meristeles differs considerably from the case above described. Neverthless, its essential structure is almost the same.

The solid construction of the stem in this part is as follows. On the stelar wall, numerous leaf-gaps are arranged in the same way as the leaf-scars; the gaps are compressed together, and each gap flattens considerably compressed in vertical direction, that is, it is only about 30 mm. in vertical length. The stelar margins at the gap curve outwards considerably, and the leaf-traces are parted consecutively from the margins, crowded together. The medullary bundles become as many as 270, and those on the peripheral part are buried in the grooves of the sclerenchymatous sheath of the stele. The course and mutual connection of the medullary bundles are also the same as in the case above mentioned, but owing to the shortening of the gap, these processes are accomplished quickly. Cortical bundles are found four to six in each meristele, one pair of them belonging to each gap. It must be mentioned here that, the cortical bundle fuses with the leaf-trace belonging to the superior series, situated at the lateral corner, and on its way does not connect with the leaf-trace belonging to the inferior series, though sometimes, a temporary fusion, such as is found in the case above mentioned, takes place.

D. Histological Structure of the Stem

The histological structure of the stem is of the normal Cyatheacean type. The epidermis and superficial tissue usually fall off, but in some parts these tissues sometimes persist. In a cross section, the superficial tissue with a thickness of a few mm., is brownish, and its external part projects outwards so as to form scales. On the inside of the epidermis is a layer composed of parenchyma, which passes into the sclerenchymatous layer composed of fibers (Fig. 44). When the outer tissues fall off,

the separation occurs at the middle part of the parenchyma. The sclerenchymatous sheath enclosing the meristele is composed of sclerenchymatous fibers. The region between this layer and the hypodermis (3–5 mm. in thickness) and that between this and the meristele (2–4 mm. in thickness) is the cortex proper consisting of whitish parenchymatous cells, and also including mucilage sacs. At the boundary between the sclerenchymatous layer and the cortical parenchyma, a layer of peculiar cubical cells is constantly found (Fig. 44, cc).

The stele, with a breadth of about 3 mm., is constructed on the normal Cyatheacean type; surrounded by an endodermal layer, there is a concentric bundle. At the external part of the phloem is a layer of tangential cells.

The pith consists of the same tissue as the cortex including some mucilge sacs.

The structures of the medullary and cortical bundles coincide; they are both protostelic, and when they are small the central xylem consists entirely of a mass of tracheids. In the larger bundles a parenchymatous pith is included within the tracheidal mass, and in the largest a small intercellular space is found within the pith.

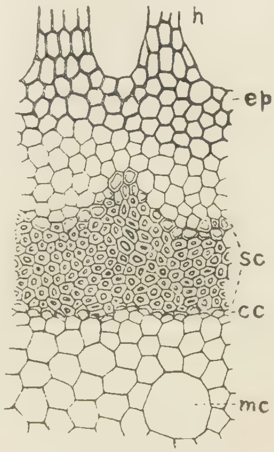

Fig. 44. Cross section through the external part of a stem. (magnified)
h, hair
ep, epidermis
sc, sclerenchyma
cc, cubical cells
mc, mucilage sacs

E. Structure of the Leaf

Large leaves attain a length of 3 meters. Throughout the petiole and rachis, the surface is greenish and is ornamented with small protuberances. A cross section of the petiolar base of a large leaf shows a semicircular outline, flattened at the upper side, with a transverse diameter of 45 mm. Tracing the petiole upwards, its outline becomes gradually smaller and more circular (Fig. 45, A–D).

The mode of arrangement of vascular strands in the petiole and rachis differs in different parts (Fig. 45). In the part with larger sized petiole, the strands are abundant, there being 60–70 of them. In the petiole, most of the strands run parallel to the petiolar surface; besides, on the lateral sides two rows of strands project inward and downward, those of the upper row being more numerous (6–10 pairs in number)

than those of the lower (1–3 pairs). In addition to these, on the upper part there are some isolated strands (1–3 pairs). Marked by the laterally projecting series of strands, the petiolar strands are classified as the superior and inferior series (Fig. 45, A). Tracing the petiole upwards, separate strands fuse together side by side, giving a wavy outline in cross section. At the middle part of the petiole, the bundles of the superior and inferior series are respectively connected, the former in a triangular and the latter in a semicircular form; also within the former there are two rows derived from the isolated bundles (Fig. 45, B). Somewhat higher up, the median part of the upper arc opens, and both ends connect with the isolated bands in a hook-form, while the lower arms elongate considerably and approach each other. At the same time, the median part of the inferior arc opens, and the ends turn a little inwards (Fig. 45, B–C). The completion of four such bands occurs usually at the lower part of the rachis or at the upper part of the petiole. Further up, the lower arms of the superior bands come into contact with each other in a V-shape (Fig. 45, D), while the lower series are combined in a single band; this last form is maintained up to the summit of the rachis.

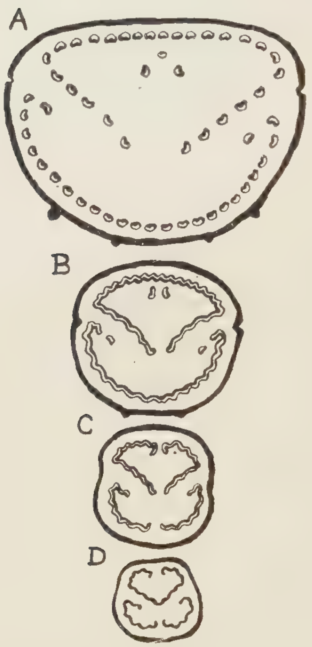

Fig. 45. Cross sections of different four parts of a leaf-axis showing the mode of arrangement of vascular strands. (nat. size)

A, Base of the petiole
B, Middle of the petiole
C, Top of the petiole
D, Middle of the rachis

In the base of a large pinna-axis four strands are present, arranged in the same way as in the upper part of the rachis. The branching of the pinna-traces from the rachis-bundles takes place according to the so-called extra-marginal type. In the branching region, a small strand connects the two series of traces.

The histological structure of the leaf is of the normal Cyatheacean type. In the petiole, under the epidermis and separated by a layer of parenchyma, is a layer of fibrous tissue. Each separate bundle is V-shaped, and in it the central xylem is enveloped by the phloem. The wavy bundle is the connection of these V-shaped bundles, and exhibits no essential difference.

F. Structure of the Root

Roots grow out from all sides of the stem, but those from the higher part of the stem are too short to reach the ground, and only those of the basal part serve as absorbtive organs. The latter are entangled with each other forming a thick root-mass. They spring from the stem in a regular manner. Their mode of origin is most conveniently studied from the position of the remains of roots, which are situated under the leaf-scars. The length of the root-area under a leaf-scar is two or three times as long as the scar itself. The parting of the root-traces takes place in the lower half of the stelar margin at the leaf-gap. They part from the stelar margin or from the bases of leaf-traces just parted. Descending obliquely through the outer cortex, they leave the stem as root-bundles. In the higher part of the stem where the leaf-scars are crowded, the roots are not usually found. The vascular bundle of the root is typically diarch.

II. The Young Plant

In young individuals, the stem tapers conically toward the lower end, and is invested with a thick root-mass. Leaves fall off from their bases, but the separating planes are not at the same level as the stem surface, being elevated on the lower side. The elevation, however, becomes less prominent toward the upper and thicker portion of the stem.

In order to see the size and arrangement of leaf-gaps as well as the origin and course of medullary and cortical bundles, the writer examined the internal structure of two young plants. In the main points, both plants exhibited no difference of structure, and accordingly, let us take for description a case based on material showing a very good growth. The results to be given below were obtained from studying serial cross sections made through the portion within 130 mm. from the basal tip.

A. Cross Sections of the Stem

At first, the structure will be considered in eight main parts of the stem at different levels, in order to get a general idea of the structure of the stem.

Region A (3 mm. from the lower tip ; diameter 3 mm. ; Fig. 47, A). This region has an irregular outline, and the stelar ring is divided by two leaf-gaps, from each of which one pair of leaf-traces is detached. No sclerenchymatous sheath is found surrounding the stelar ring (Fig. 46, 1). Neither medullary nor cortical bundles are found.

Region B (6 mm. from the tip; diameter 6 mm.; Fig. 47, B). The outline of this region is irregularly triangular, and the stelar ring is interrupted by two gaps, each with two pairs of leaf-traces. Incomplete sclerenchymatous tissue is found on both sides of the stelar ring (Fig. 46, 6–8). Three medullary bundles are found, but no cortical bundles.

Region C (13 mm. from the tip; diameter 11 mm.; Fig. 47, C). This region also is triangular, and there are three gaps in the stelar ring. Three pairs of leaf-traces are parted from each gap. Fifteen medullary bundles are found, but cortical bundles are absent.

Region D (27 mm. from the tip; diameter 15 mm.; Fig. 47, D). The outline of the stem and the stele has a rounded triangular form. In the stelar ring three gaps are found, each having five or six pairs of leaf-traces. Twenty medullary bundles are found, but no cortical bundles.

Region E (48 mm. from the tip; diameter 23 mm.; Fig. 47, E). General structure like that of the former; seven or eight pairs of leaf-traces to each leaf-gap. Number of medullary bundles reaches twenty-six, but cortical bundles are not found.

Region F (67 mm. from the tip; diameter 36 mm.; Fig. 47, F). The outline of both stem and stele is triangular. Each leaf-gap gives off nine pairs of leaf-traces. Number of medullary bundles reaches thirty-seven, of which those in the peripheral part are buried somewhat in the grooves of the sclerenchymatous sheath. No cortical bundles are found.

Region G (95 mm. from the tip; diameter 53 mm.; Fig. 47, G). The stem in cross section is pentagonal, and the stelar ring tetragonal, with three gaps. About fourteen pairs of leaf-traces are found in each leaf-gap. Medullary bundles become as many as seventy, and their course is similar to that in the adult plant. The bundles situated in the periphery are buried in the grooves of the sclerenchymatous sheath. It is here that the cortical bundle makes its appearance. In this region, eight cortical bundles are found, of which six are near the leaf-gaps, and other two in contact with the sclerenchymatous sheath.

Region H (122 mm. from the tip; diameter 60 mm.; Fig. 47, H). The outline of the stem and the stele is rounded triangular. There are four leaf-gaps, with about seventeen pairs of leaf-traces. Medullary bundles reach as many as one hundred and four, and those in the peripheral part enter deeply into the grooves of the sclerenchymatous sheath. Cortical bundles are nine in number; most of them are situated in contact with the sclerenchymatous sheath, and dip somewhat into it.

B. Solid Construction of the Stem

The solid construction of the stem of this young plant was studied by a comparison of serial cross sections.

a. The Stele

Though the stele is originally cylindrical tube, it becomes irregular owing to the projection of the marginal parts of the meristeles at the leaf-gaps. Usually, three leaf-gaps overlap in a cross section, so that the stelar ring is triangular in cross section. The relation of the size of the stele in any region and the distance of that region from the basal tip may be seen in the following table:

Region	A	B	C	D	E	F	G	H
Distance from the tip (mm.)	3	6	13	27	48	67	95	122
Diameter of the stem (mm.)	3	6	11	15	23	36	53	60
Diameter of the stele (mm.)	1	3	7	10	15	24	35	45

The size of the stele gradually increases upwards, but in Region E, the rate of increase slightly diminishes. This relation is more clearly seen in the diagrammatic figure showing the developing of the stelar tube (Fig. 47).

b. The Sclerenchymatous Sheath

The sclerenchymatous sheath on both sides of the stelar ring is not found at the very base of the stem. It develops gradually on both sides of the ring in separated masses, which become connected gradually so as to form a continuous sheath (Fig. 46).

c. The Leaf-Gap

The size of the leaf-gaps in the main regions is as follows:

Region	A	B	C	D	E	F	G	H
Length of the gap (mm.)	1	2	3	7	11	16	20	22

It is seen from this table that the size increases upwards in keeping with the increase of the diameter of the stem (Fig. 47).

The phyllotaxy or arrangement of the gaps will now be considered. The gaps are regularly arranged in a radial manner, but the arrangement is not constant throughout the entire length. In the lower part it is in a $\frac{2}{5}$ system, but changes gradually into a $\frac{3}{8}$ system (Fig. 47).

d. The Leaf-Trace

The number of leaf-traces in each gap increases upwards in keeping with the size of the stem or gaps. Usually, some of the traces bifurcate in the cortex, so that, the number of vascular strands in the petiole is larger than that of the parted traces. The former can be estimated by the number of strands in a leaf-scar. This relation is shown in the following table:

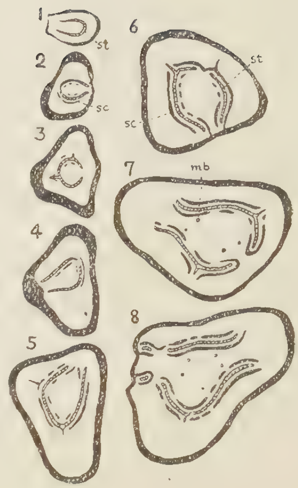

Fig. 46. A series of cross sections at the basal part of a stem, showing the mode of formation of the sclerenchymatous sheath. (×2)

st, stele
sc, sclerenchymatous sheath
mb, medullary bundle

Region	A	B	C	D	E	F	G	H
Number of leaf-traces (in pairs)	1	2	3	5	6	9	10	12
Number of petiolar strands (in pairs)	1	2	3	6	7	11	14	17

The arrangement of strands in each scar differs considerably in each region. In the case with less than four or five pairs of strands, they are arranged in a simple circular form, but in the case with six pairs (three superior and three inferior) one lateral pair projects somewhat inwards, corresponding to the first pair of the superior strands. Upwards, with the increase of the number of strands, those projecting increase in number, and when they reach nine pairs, four of the inferior series are arranged in an arc, while out of five pairs of the superior series three pairs form the upper arc and two lateral pairs project inwards. The projection becomes more and more prominent, and at the same time, one pair in the median upper part begins to project inwards. In this way, the number of vascular strands increases gradually upwards, until in the petiole in the upper part of the material (Region H), seventeen pairs are present, of which six pairs belonging to the

inferior series are arranged in an arc, and the lateral uppermost one projects a little inwards, while out of eleven pairs of the superior strands seven pairs form the upper arc, and three lateral pairs and one upper pair project inwards respectively.

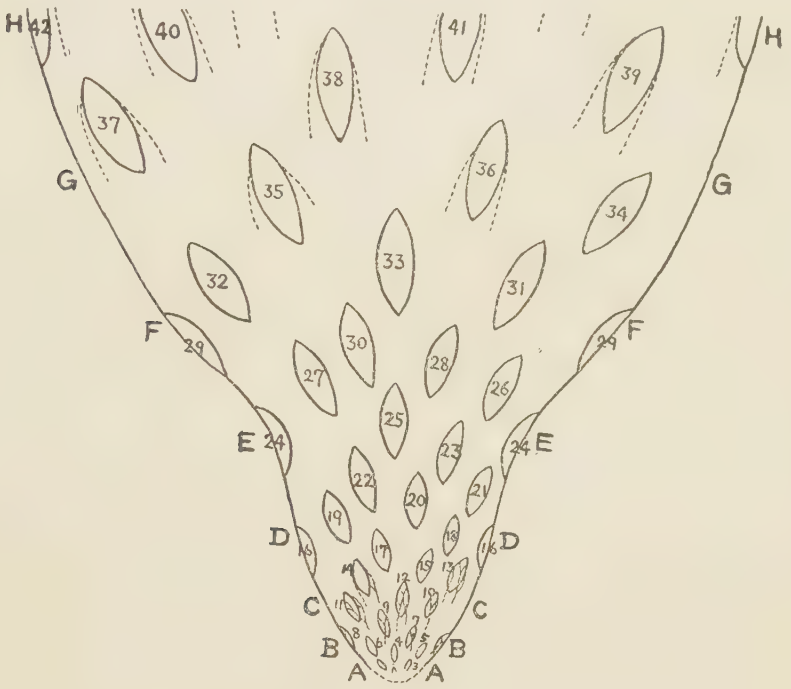

Fig. 47. Diagrammatic figure of the stelar wall of a young plant, showing the size and arrangement of leaf-gaps (1–42), the course of the medullary and cortical bundles (dotted-lines). Medullary bundles are omitted above Region D. Cortical bundles appear above Region G. A–H show the eight regions referred to in text. (nat. size)

In a word, the mode of parting of leaf-traces in the young plant is nearly the same as in the case of other species, but as the traces are numerous in this plant, their courses become complex early in the young part.

e. The Medullary Bundle

In the adult plant, medullary bundles are very numerous and form a very complex network. Anastomosis begins early even in the lower tip of the stem, so that the complete course of the bundles is hardly traced.

In the first place, the number of strands in the main regions will be mentioned in the following table :

Region	A	B	C	D	E	F	G	H
Number of medullary bundles	0	3	15	20	26	37	70	104

It is in a part a little below Region B that the medullary bundle first appears. A bundle which appeared near the bottom of the 7th. gap ascends a little and bifurcates, and the two branches fuse to the two sides of the gap. Three bundles in the following three gaps (8th.–10th.) take the same course. In the next gap (11th.), a bundle which has appeared in the pith bifurcates, then both branches bifurcate again, and these two pairs connect with two pairs of leaf-traces of the gap (Fig. 47). In the following gaps, the medullary bundles repeat the same process, but sooner or later, mutual connection of the bundles takes place, and makes it difficult to trace their courses completely, and therefore, in the Fig. 47, the course of the bundles above Region D is omitted. Arguing from the case of other species, it may be assumed that, all of the medullary bundles appear in the pith and ascend through it, branching and connecting with each other, until they come in contact with the stelar margins at the leaf-gaps, and give rise to some of the leaf-traces belonging to the superior series. Their fusion with the stele affects the latter. In some lower gaps, the medullary bundles terminate as one pair, but tracing the gaps upwards, they terminate as two and then as three pairs, and so on. At the same time, they anastomose with each other, and their number becomes irregular, which makes it difficult to count the exact number of branches which connect with a leaf-gap. The following table roughly shows their number :

Region	A	B		D	E	F	G	H
Number of medullary bundles in connection with the leaf-gap (in pairs)	—	1	2	2	3	4	5	6

All of the medullary bundles connect with leaf-gaps belonging to the superior series, the first bundle with the first trace or the laterally projecting one, the last with the last or upper median trace of the upper arc, and the intermediate ones, if present, with the intermediate traces. But, some branches of the bundles run through the gap directly to the petiole, in which they have isolated positions in the upper part.

f. The Cortical Bundle

The appearance of the cortical bundle takes place on both sides of the 35th. gap, situated a little below Region G, i. e. about 90 mm. distant from the base. Each of them ascends a little accompanied by the sclerenchymatous sheath, and fuses with the stelar margin at the gap, the fused part being separated as a leaf-trace situated at the lateral corner of the superior series. In following some gaps, the course of the cortical bundles is nearly the same, but they gradually become longer (Fig. 47). At lower levels, the bundles are hardly distinguishable from the root-traces, but in upper levels they are easily recognized as they are situated in contact with the outer surface of the sclerenchymatous sheath of the stele, as in the adult plant.

Summary

1. The stem of *Alsophila Bongardiana* is tapering at the lower end, where it is thickly covered with roots. It reaches a height of 10 meters or more.

2. The leaves are borne on the stem apex, and older ones fall off from their very bases leaving the characteristic scars on the stem surface. The phyllotaxy is $\frac{2}{5}$ in the young part, but changes gradually upwards to $\frac{3}{8}$, and then proceeds in an irregular manner to the system of arrangement in ten or more vertical rows.

3. The surface of the stem is covered with scaly hairs. The hypodermis consists of the outer parenchymatous and inner sclerenchymatous layers. The superficial layer on the outside of the parenchyma usually falls off.

4. The central cylinder of the stem is dictyostelic. The margin of the meristele at the gap turns outwards, and gives off the leaf-traces consecutively.

5. A meristele is constructed according to the normal fern-type, i. e. the amphicribral concentric type. Outside the phloem, is a layer of tangential cells. The sclerenchymatous sheath of the stele is composed of sclerenchymatous fibers. In the fundamental tissue, some mucilage sacs are present.

6. The leaf-gap is fusiform, and the stelar margins at the gap turn outwards considerably. The marginal turning disappears at the upper part of the gap, and the traces detached from the lower part of the recovering region belong to the inferior series, while those from the upper part belong to the superior series.

7. In the case of a larger petiole, about seventy vascular bundles are present, most of which are arranged in a ring along the petiolar surface; besides, two laterally projecting rows and an upper isolated group are found. In a small petiole, the vascular strands are few in number, and are simple in arrangement.

8. Ascending the petiole, the vascular strands fuse together side by side into four wavy bands, which in the rachis are combined into three, and then into two. The branching of pinna-traces takes place according to the extra-marginal type.

9. Under the epidermis of the petiole is a hypodermal layer composed of sclerenchymatous fibers. The petiolar strands are of the normal fern-type in structure.

10. Root-traces are parted from the stelar margins at the leaf-gaps, and penetrate through the cortex obliquely downwards. Roots have the diarch radial bundles.

11. Medullary bundles appear early in the young part. They gradually increase in number upwards, until in the adult part they amount nearly two hundred and fifty in a cross section. They appear independently in the pith, and their upper ends fuse with the stelar margins at the gap. In their course, they connect with each other, and form a network. The first bundle belonging to a leaf-gap fuses with the first leaf-trace of the superior series, the last with the last trace, and the intermediate bundles with the intermediate traces. Some branches of the medullary bundles enter the petiole directly, and are isolated in its upper part.

12. One pair of cortical bundles belongs to each leaf-gap. They arise in the cortex, and ascending through it fuse with the stelar margins at the gap, the fused parts being separated as a pair of leaf-traces situated at the lateral corners of the superior series. In their course, they connect temporarily with the traces of the inferior series.

13. Cortical and medullary bundles are constructed according to the same type, i. e. the protostelic type. In the smaller bundles, the xylem consists of a tracheidal mass, while in the larger it includes a parenchymatous pith; in some cases there is a cavity in the pith.

14. The stelar system of *Alsophila Bongardiana* is similar to the 'Cyathean dictyostele', but differs from it in having the cortical bundles. The present type of the stelar system will be called an "Alsophilan Dictyostele"

VI. Additional Note on Cyathea spinulosa, Wall.*

In Japan, the genus *Cyathea* so far as is known is represented by only a single species, *Cyathea spinulosa*, WALL. It is found in Hachijô, the Bonins, the Gotô Islands, the Koshiki Islands, the Ôsumi and Satsuma Peninsulas, the South-West Islands, the Loochoos and Formosa. It is known to occur also in South China, the Maley Archipelago and India. The most characteristic features of this species is the presence of spines in the petiole.

On the anatomical structure of the species, a description based on material obtained from Hachijô has been already given in Part II. Later, on the occasion of a botanical trip to the Bonins and Formosa, the writer found that the plants growing in both of these islands show, in the structure of the stems, certain differences from those of Hachijô. Consequently, the question arises as to whether the materials from different regions represent really a single species or comprise different species or varieties. In order to decide this point, plants collected in the following localities were subjected to a close study.

Locality	Lat. (N)	Long. (E)	Date of collection
Hachijô Island, Idzu	33° 5′	139° 50′	Apr. 1924
Chichi-jima, Bonin Is.	27° 5′	142° 10′	Jan. 1925
Fukai-jima, Gotô Is.	32° 40′	128° 40′	Jan. 1926
Konejime-mura, Ôsumi	31° 10′	130° 45′	Jan. 1926
Ôshima, Kagoshima	28° 20′	129° 30′	Jan. 1926
Kuntian, Okinawa Is., Loochoo	26° 40′	128° 20′	Dec. 1925
Sôzan, Taihoku, Formosa	25° 10′	121° 30′	Aug. 1925

Of these materials, the stems of similar size, viz. 60–80 mm. in diameter, were chiefly used for comparison. In cross section, they exhibit great diversities of structure according to different sources as given below.

a. Material from Hachijô. The sclerenchymatous sheath on both sides of the meristele shows a smooth outline. No cortical bundles are found (Fig. 48, A).

b. Material from the Loochoos, Ôsumi and the Bonins. The sclerenchymatous sheath on both sides of the meristele is influenced by

* The contents of the Part VI appeared in Japanese in the Bot. Mag. Tokyo, Vol. 40, pp. 307-310, May 1926.

the protrusion of medullary bundles, forming an irregular denticulation, and sometimes it is cut off. No cortical bundles are found. (Fig. 48, C).

c. Material from the Bonins and Ôshima. The sclerenchymatous sheath is the same as in the case b, but some cortical bundles are found (Fig. 48, B).

d. Material from Formosa. The sclerenchymatous sheath is the same as b. No cortical bundles are found. The meristele curves prominently in a horseshoe-shape (Fig. 48, D).

Judging from the case of *Alsophila*, these anatomical differences, especially the presence or absence of the cortical bundles, may be considered as deserving a specific difference. For convenience sake, these types may be called (a) Hachijô-, (b) Loochoo-, (c) Bonin- and (d) Formosa-types, although there are intermediate forms, showing that these types are not absolute ones.

The general anatomical structure in cross sections of the stems of some materials from different localities will be shown in the following table:

Locality	Diameter of the stem(mm.)	Diameter of the stele (mm.)	Number of leaf-gaps	Number of medullary bundles	Number of cortical bundles	Interruptions of sclerenchy. sheath
Hachijô	62	43	5	55	0	0
Bonin (a)	75	50	8	92	18	0
(b)	100	65	13	132	90	0
Gotô	50	30	5	48	0	0
Ôsumi (a)	85	60	8	109	0	1
(b)	110	70	10	161	24	4
Ôshima (a)	55	37	5	42	1	2
(b)	75	43	10	117	1	8
Loochoo	65	45	8	84	0	2
Formosa	62	32	8	70	0	0

A. Curvature of the meristele. The phyllotaxy or position of the leaf-gaps differs at various levels in one and the same individual, so that to these characters no diagnostic value can be assigned. The curvature of the meristele in cross section increases in proportion to the mutual approach of the leaf-gaps. In the part of the stem with loosely arranged leaves, the stelar margins facing the leaf-gap curve outwards, and the stelar body itself remains uncurved, while in the part with closely arranged leaves, the meristele itself is short and curves in an arc form. The latter form may be seen in the higher parts of the stem. But, in the Formosa-type the curvature of the meristele is remarkable, even in the young stem (Fig. 48, D). The ratio of the diameter of the stem to that of the stelar ring is more than 1.9 in the Formosa-type, while in other types it is 1.4–1.6.

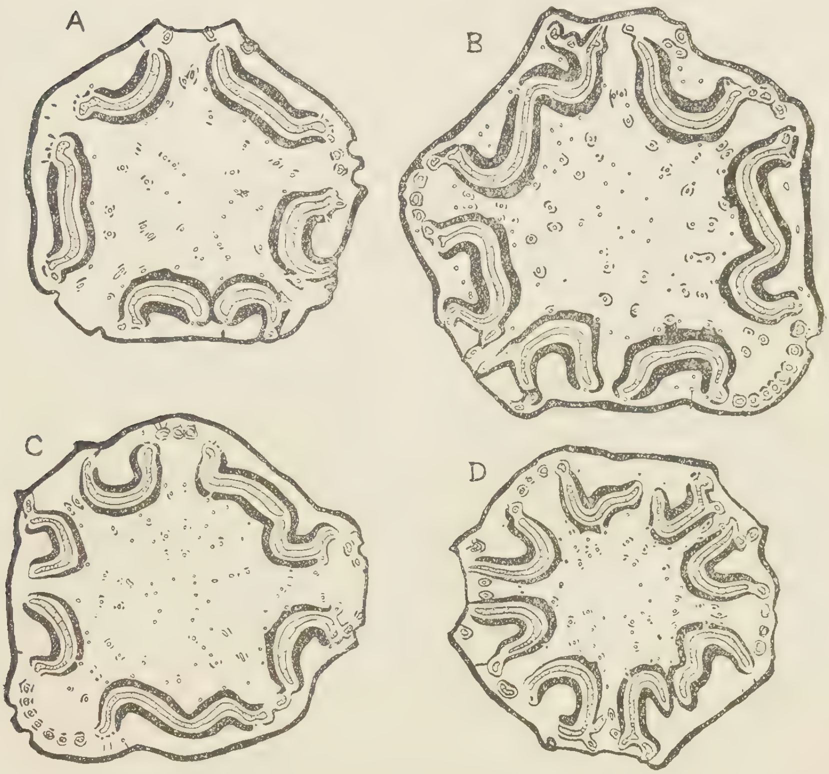

Fig. 48. Cross sections of the stems of *Cyathea spinulosa* from different localities, showing variation of structure. $(\times \frac{2}{3})$

A, Stem from Hachijô C, Stem from the Loochoos
B, Stem from the Bonins D, Stem from Formosa

B. The sclerenchymatous sheath of the meristele. The brown sclerenchymatous sheath which surrounds the meristele, runs nearly parallel to the latter, and has the same outline. The surface of the sheath facing the pith is sometimes irregularly denticulate, being influenced by medullary bundles. In extreme cases, the sheath is interrupted by medullary bundles. The Hachijô-type shows no such denticulation, while in other types the sheath-outline is always denticular, and sometimes is interrupted at some points (Fig. 48). In *Alsophila*, the presence or absence of such denticulations and interruptions may be used, to a certain extent, as a basis for specific identification. In the present case, however, both forms may be found among the plants found in the same locality, or even in different parts of the stem of one and the same individual. Generally speaking, the denticulation and interruption are not prominent in the smaller or younger stem.

Fig. 49. Cross section of a stem of *Cyathea spinulosa* from the Bonins at the level with leaf-scars arranged in ten vertical rows, showing the stele segmented in ten meristeles, the interruption of the sclerenchymatous sheath and the presence of the cortial bundles. $(\times \frac{4}{5})$

C. The cortical bundles. Medullary bundles are present abundantly in all types. Cortical bundles are found in the Bonin-type (Figs. 48 & 49), but they are absent in other types, even in the stem of the same size as that of the Bonin-type. In a stem of the Bonin-type, with a 74 mm., there are found eighteen cortical bundles (Fig. 48, B), while in another stem, with a diameter of 100 mm., they amount to nearly one hundred. In the stems of other types, none or only a few cortical bundles are found, as is shown in the above table. A stem from Ôsumi, with a diameter of 110 mm., contained twenty-four bundles. Judging from these facts, it is evident that the presence of the cortical bundles is inconstant in this species, and therefore, the presence or absence of them may not be considered as a specific difference. In gereral, the cortical bundles are not found in the younger part, but may appear when the stem reaches a certain size. This relation is well illustrated

by a stem from Ôsumi; in its basal part no cortical bundles are found, while in a somewhat higher part twenty-four of them are found.

As the cortical bundle is not accompanied by the sclerenchymatous sheath, its presence and position are difficult to recognize at first sight, especially, the bundle near the leaf-gap is very difficult to distinguish from the root-trace. The course and position of the cortical bundle are somewhat irregular, and the number of bundles belonging to each gap is also inconstant. The bundle appears in the cortex, and ascending through it fuses with the stelar margin at the leaf-gap. In its course, it coalesces with other bundles. The upper end fuses with the lateral corner of the inferior turning of the stelar margin, but its fusion has no important influence on the stelar form.

In the histological structure of the stems, the types present no essential differences. The arrangement of petiolar bundles is also the same in all types.

Summary

1. The outline of the sclerenchymatous sheath of the stem stele of *Cyathea spinulosa* may or may not be influenced by medullary bundles. In the former case, it shows irregular denticulations, and sometimes is interrupted forming small gaps.

2. In the stem of *Cyathea spinulosa*, cortical bundles may or may not be found. Their occurrence is inconstant, and their number is also inconstant. They appear in the cortex, and ascending through it fuse with the stelar margins at the leaf-gap belonging to the inferior region. They branch sometimes, and connect with one another.

3. *Cyathea spinulosa* in Japan shows some types different in structure, but these types are not distinctive, as there are intermediate types between them. So far as the form of the meristele is concerned, however, the plant from Formosa represents a type differing from the plants of other regions.

VII. Cibotium Barometz, Sm.*

Cibotium Barometz is a Cyatheacean species distributed widely in the tropical regions of Asia, such as the South-West Islands of Japan, South China, Malacca, etc.

For the purpose of anatomical investigation, the writer collected the greater part of his material at Sôzan, near Taihoku, Formosa, in August 1925, but some materials were also collected at Okinawa Island, the Loochoos, in December 1925.

The stem is short and always creeping. Its surface is covered closely with long golden hairs. Leaves and roots emerge from all sides of the stem, the former growing upwards and the latter downwards. The leaves have tripinnate laminae, the underside of which has a whitish appearance.

The anatomical structure of this plant has been given by certain authors. Parmentier (1899) studied the vascular strands of the petiole, but touched on no other points. Gwynne-Vaughan (1903) figured a diagrammatic solid model of the stele, showing the form of leaf-gaps and the mode of branching of leaf-traces. According to his figure, the stele has a form intermediate between a solenostele and a dictyostele, but he gave no detailed explanation. Bower (1921) gave a figure of a cross section of a stem, showing the circular stele with no sclerenchymatous sheath.

A. Cross Section of the Stem

A cross section of a stem gives an irregular outline owing to the attachment of petioles (Fig. 50). The outline of the stem is circular, but the petiolar bases are relatively large, in some cases being nearly as thick as the stem itself, so that in the cross section of such a part, the petiolar base bulges out of the stem considerably (Fig. 50). Moreover, the bases of two or three leaves may occur in the same cross section of the stem, thus giving its outline an irregularly rugged form. In a plant of moderate growth, for example, the stem itself may have a diameter of 27 mm., while the petiolar base may bulge out about 20 mm., and at a level where two leaves are situated side by side on the stem, the

* The contents of the Part VII appeared in Japanese in the Bot. Mag. Tokyo, Vol. 40, pp. 349-359, June 1926.

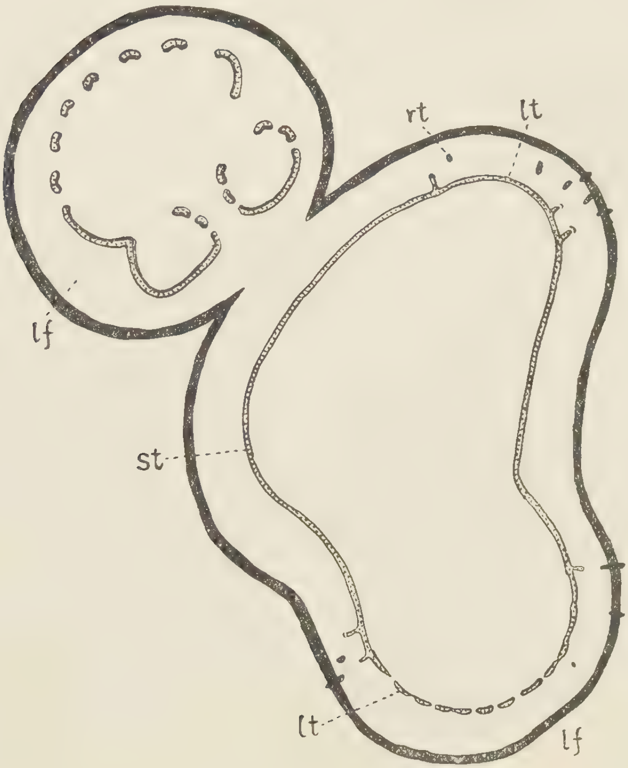

Fig. 50. Transverse section of a stem with petiolar bases.
(nat. size)

st, stele rt, root-trace
lt, leaf-trace lf, leaf-base

cross section takes an oblong shape, with the long diameter as much as 65 mm. The largest stem observed by the writer has a diameter of 50 mm.

The outline of the stelar ring is circular like that of the stem; where the outline of the stem bulges out the stele follows it, the bulging part of the stelar ring is also constricted out of the ring leaving a leaf-gap (Fig. 50, st). At the outside of the bulging part of the stelar ring, numerous root-traces are found (Fig. 50, rt). The fundamental tissue is composed of whitish parenchyma, and no sclerenchymatous sheath is found on either side of the stelar ring.

B. Solid Construction of the Stem

The solid construction of the stem was studied by means of consecutive cross sections through a length of 20 mm. in a stem of

moderate size. In this part of the stem, there are four leaves, and the stele has four gaps arranged according to a type intermediate between $\frac{2}{5}$ and $\frac{3}{8}$. Their arrangement is not influenced by the creeping habit of the stem.

All of the leaf-gaps show the same structure (Figs. 51 & 52). Following a gap from the base toward the apex, the stelar ring bulges out together with the bulging of the stem surface. Such a part can be easily recognized, as its exterior is provided with numerous root-traces (Fig. 51, 1). The bulging of the ring becomes more and more prominent, until the part is nearly of the same size as the stele itself (Figs. 50 right lower part & 51, 2–3). Then, the lateral sides of the bulging part thicken, and from each inner surface of the thickened portion of the stelar ring a new stelar branch arises projecting into the central portion of the bulging part in a hook (Fig. 51, 3–4). The outer part of this constriction corresponds to the leaf-trace. Following it still further forwards, the heart-shaped trace becomes separated from the stem stele as an independent leaf-trace (Fig. 51, 4–5). The stelar ring is interrupted by the parting of the trace. This interrupted part is the leaf-gap, which becomes narrower and narrower, and then is closed entirely (Fig. 51, 6–7).

Fig. 51. A series of cross sections of a stem through a leaf-gap, showing the mode of parting of leaf-traces. (nat. size)

Explanations in text.

Prior to this, when the stelar part bulges out in a semicircular form, or a little below the appearance of the lateral constrictions, the outer median part of the bulging trace is divided into short arcs (Fig. 51, 2–3). The division propagates laterally, and when the trace is separated from the

stem stele in a heart-shape, the division takes place in the curved margins, so that, when the trace leaves the stem it is divided into twelve or more pairs of separate strands (Fig. 51, 6–8). At the same time, some of the divided strands on the lateral sides begin to project a little inwards (Figs. 50 right upper part & 51, 7–8).

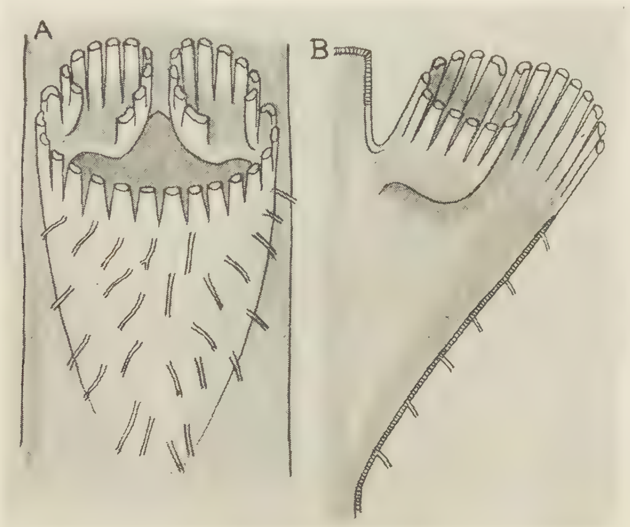

Fig. 52. Reconstruction of a leaf-gap, showing the mode of parting of leaf- and root-traces. (nat. size)

A, External view

B, Radial longitudinal'section through the median line

In this way, the leaf-trace which is detached from the stelar ring as a continuous band is divided into numerous strands, so that no distinct boundary separating the stelar ring from the leaf-trace is found (Fig. 52). When the bulging advances and the lateral constrictions occur, the limits of the leaf-trace can bė recognized exactly. A little further forwards, the trace is detached from the stele, leaving a leaf-gap on the latter. Therefore, the gap has a fusiform shape as in *Alsophila* and *Cyathea,* but it is distinguished from of the latter by the absence of the distinct limit on the lower side.

Two or three leaf-gaps overlap usually in a cross section, so that the stele is dictyostelic, but sometimes a solenostelic condition is found.

The root-traces are parted from the stele at the part where the latter bulges out to form the leaf-trace (Figs. 51 & 52). In other words, the parting of the root-traces is associated with the leaf-gap or the leaf-trace.

C. Structure of the Leaf

Large leaves of this species attain a length of 3 meters, of which the lower half or one-third is the petiolar part. The lamina is tripinnate. In the young stage, the leaves, like the stem, are covered with long golden hairs.

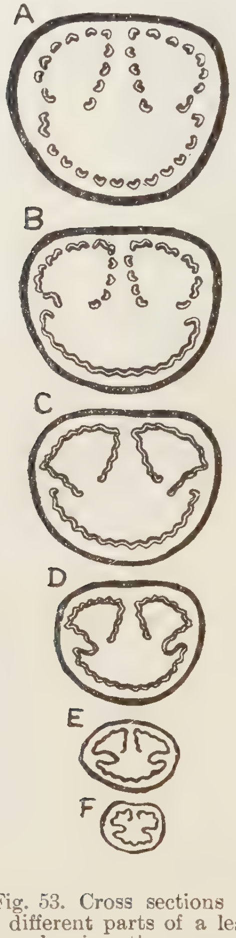

Fig. 53. Cross sections of six different parts of a leaf-axis, showing the arrangement of vascular bundles. (nat. size)

A, Extreme base of the petiole
B, Base of the petiole
C, Middle of the petiole
D, Top of the petiole
E, Base of the rachis
F, Middle of the rachis

In a cross section at the extreme base of the petiole of a moderate size, the outline shows a semicircular form flattened at the upper side, with a diameter of 20 mm. There are about twenty pairs of vascular strands, most of which are arranged in a semicircular form parallel to the surface; there are also some pairs of strands projecting inwards from the upper median side (Fig. 53, A). On each lateral side there is an interrupted part, and the strands which border this curve a little inwards. These parts are the limit of the superior and inferior series; the latter consists of about six pairs arranged semicircularly, and the former of about twelve pairs, each arranged in a triangular form. The part where the strands are in separated condition is short, and at a level a little above the petiolar base, the separate strands join end to end in a wavy form. For the first time, the inferior strands are connected in a semicircular band, and then the superior in two triangular bands (Fig. 53, B–C). The lateral interrupted parts, i. e. the limit of the superior and inferior series, remain open. The mutual connection of the strands does not affect the position of the original strands; the wavy connected bands have the same outline as the separate strands.

A little higher up, the lateral interrupted parts are also connected so as to form a single continuous band, but these parts are easily distinguished by the formation of grooves (Fig. 53, D). A connection of the strands takes

place for a short distance from the petiolar base, and throughout the greater part of the petiole and rachis, a single connected form is always seen (Fig. 53, E–F). Tracing it further upwards, the vascular band becomes smaller, and the number of its flexures decreases.

The vascular bundle of a pinna-axis is of the same type as that found in the upper part of the rachis ; it consists of a small heart-shaped band with upper and lateral projections. In the branching of pinna-traces from the rachis-bundle, both lateral corners bordering the lateral grooves of the latter bulge out (Fig. 54, 1–2), and these parts are then constricted off (Fig. 54, 3–5). The upper trace opens at the upper median part in an arc, while the lower one assumes a ring-shape (Fig. 54, 3–5). These two traces approach, and fuse into each other, and the fused trace is transformed into a peculiarly curved arc-shaped bundle (Fig. 54, 5–6).

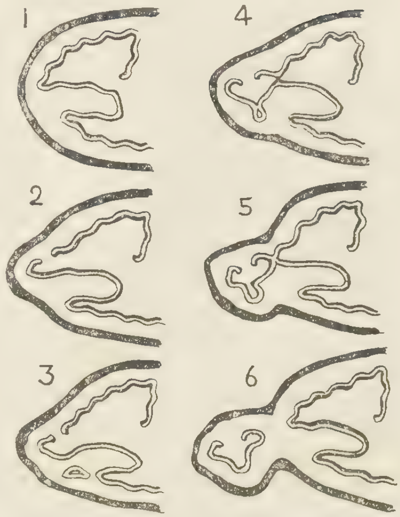

Fig. 54. A series of cross sections of a rachis through the base of pinna-axis, showing the mode of parting of pinna-traces. (nat. size)

Explanations in text.

D. Histological Structure of the Vegetative Organs

The histological structure of the stem is simpler than in *Alsophila* and *Cyathea*. The surface of the stem is covered with long golden hairs, some of which are as long as 30 mm. (Fig. 55, h). On the surface, there is a layer of thin-walled parenchyma, and beneath it, is a layer of thick-walled fibrous elements (Fig. 55, sc). The fundamental tissue consists of whitish parenchymatous cells containing no mucilage sacs. At the boundary between fibers and parenchyma, particular cells, such as are found in *Alsophila* and *Cyathea*, are not seen.

The meristele is relatively thin and is constructed according to the normal fern-type. The xylem occupies the central part of the meristele and consists of tracheids and parenchyma. The phloem is situated on both sides of the xylem, and on its external part there is a layer of tangential cells. The endodermis is distinct. The stele is not enclosed in any mechanical tissue.

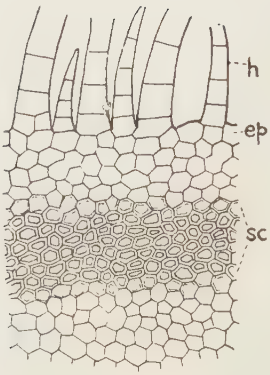

Fig. 55. Cross section of the external part of the stem. (magnified)

h, hair
ep, epidermis
sc, sclerenchyma

In the petiole and rachis, under the epidermal layer is a thick sclerenchymatous layer. The hairs on the surface are of the same type as those found in the stem. The fundamental tissue is parenchymatous. The vascular bundle is enclosed in a distinct endodermis, on the outer side of which is a thin layer of fibrous tissue. The xylem occupies the central part of the meristele showing a wavy outline, and inside the crest of each wave there is a protoxylem, usually accompanying a small cavity, which is sometimes filled with tylosis-tissue. The phloem situated on the internal side of the xylem is somewhat indistinct.

The root has a diarch bundle and a thick cortex.

E. The Young Plant

The basal part of the rhizome tapers conically, and the surface is closely covered with hairs.

Serial cross sections of a young stem were made as far as 45 mm. from the base, and by a comparison of them the solid construction of the stem was studied.

In the first place, the general structure in four main regions in cross section will be given in the following table :

Region	A	B	C	D
Distance from the tip (mm.)	2	12	25	45
Diameter of the stem (mm.)	2	7	8	10
Diameter of the stele (mm.)	1	3	4	6
Number of leaf-gaps	1	2	2	3
Length of the leaf-gap (mm.)	3	5	8	10
Number of leaf-traces (in pairs)	1	2	2–3	3

The diameters of the stem and the stele increase nearly at the same rate from the basal tip toward the apex, also with a corresponding increase of the size of the leaf-gap.

The arrangement of leaf-gaps is always radial, notwithstanding the creeping habit of the rhizome ; it is $\frac{2}{5}$ at the base, and has a tendency to change to $\frac{3}{8}$ toward the apex of the stem.

The mode of parting of leaf-traces is similar to that in the adult stem, but is simpler than the latter. A part of the stelar ring bulges out and is soon divided into several strands. In the young part, a band-shaped trace is divided into one or two pairs of separate strands. When the vascular strands of the petiolar base are less than three pairs, they are arranged in a circular form, but in the petiole with four or more pairs of strands, one or two of these pairs on the lateral sides show a tendency to project a little inwards. The incurving becomes more and more prominent as the strands increase in number. At the same time, the projection of the strands in the median upper part makes its appearance, and gradually becomes prominent.

F. Adventitious Buds

The rhizome of *Cibotium Barometz* often bears adventitious buds. In one material two buds were found, and in another six. The formation of the bud is not a rare phenomenon in this plant, and was recorded by Bower (1912). The bud is so small in size as to be concealed under the hairs of the stem surface. It is a spherical process with a pointed apex, its length being less than 10 mm. (Fig. 56).

The vascular system of the bud is a branch of the stem stele. This branch is thin, but increases in size conically toward the bud (Fig. 57). The bundle at the lower part of the bud is constructed like a typical protostele, i. e. in the center there is a tracheidal mass which is

Fig. 56. A sketch of a rhizome with three adventitious buds (b_1-b_3); hairs have been removed. ($\times \frac{2}{3}$)

surrounded by a ring of phloem and then by an endodermis. Approaching the apex of the bud, in the center of the tracheids the parenchyma makes its appearance, followed by the internal phloem and then the internal endodermis. The solenostele thus formed broadens, and then narrows again toward the apex of the bud.

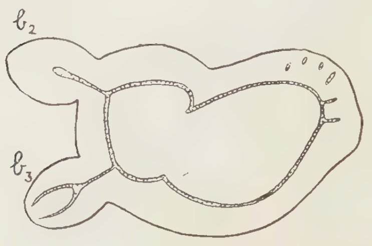

Fig. 57. Cross section of the rhizome shown in Fig. 56 through the buds b_2–b_3. (nat. size)

The bud seems to be formed in association with the bulging of the leaf-trace. It has been observed that, in some cases, two buds are formed at the base of one and the same petiole (Figs. 56 & 57, b_2 b_3). The writer has never seen the bud developed into a branch. It is possible that it develops and takes place of the stem when the latter is damaged.

G. Comparison with the Cyatheeae and the Affinity

The genus *Cibotium* constitutes together with two other genera—*Balantium* and *Dicksonia*—the tribe Dicksonieae, and is distinguished from the tribe Cyatheeae consisting of three genera—*Cyathea, Hemitelia* and *Alsophila*. The Cyatheeae include most of the Cyatheaceae, while the Dicksonieae include only a few.

Let us now compare *Cibotium Barometz* with the Cyatheeae, and consider the relation between them.

a. Creeping Habit of the Stem

The stem of *Cibotium Barometz* is always small and creeping. Most of the species belonging to the Dicksonieae have tall erect stems. In the Cyatheeae, most species have erect dendroid stems, while a few have creeping rhizomes, e. g. *Alsophila acaulis, Al. formosana*. The creeping habit of the stem, therefore, cannot serve as a criterion for the distinction of the two tribes, the Cyatheeae and Dicksonieae.

b. The Stele of the Stem

The stele of the stem of *Cibotium Barometz* is a simple dictyostele or a solenostele. All of the species of the Dicksonieae have the ordinary dictyostele, while the Cyatheeae have the dictyostele with medullary bundles, and in some cases cortical bundles too. The presence or

absence of these additional bundles is one of the distinction between the two tribes. The two tribes, however, agree in the particular form of the leaf-gap, which determines the characteristic mode of parting of the leaf-traces, and may be distinguished from that of the Polypodiaceae.

c. The Sclerenchymatous Sheath of the Stem Stele

In the stele of the stem of *Cibotium Barometz* there is no brown sclerenchymatous sheath, which is one of the characters of the Cyathea-cean stems. This sheath is found in all species of the Cyatheeae and also of the Dicksonieae; *Cibotium Barometz* is an exception in this respect. It has been stated that *Alsophila blechnoides* has not this tissue, but this species is not a true *Alsophila*-species and is included in another genus, viz. *Metaxyla*[1]. *Thyrsopteris elegans*, a monotypic species, is another example without the sheath[2]. Whether the absence of the sheath ever occurs in other species of Cyatheaceae is not known. From this point, *Cibotium Barometz* deviates from the normal Cyathea-cean species.

d. The Petiolar Bundle

The petiolar bundle of *Cibotium Barometz* consists of a continuous wavy bundle, and at a short distance in the base, this bundle consists of separate strands. Other species of the Dicksonieae have petiolar bundles of a type similar to this. In the Cyatheeae, on the other hand, it is only in the upper part of the rachis that vascular strands are connected in a wavy form, and the greater part of the rachis and petiole have the separate strands. The arrangement of the strands, however, is similar in both tribes, and may be divided into the superior and inferior series, marked by the lateral projection. The upper projection in *Cibotium Barometz* corresponds to the same projection or to the upper isolated strands of the Cyatheeae. When the mutual connection of the strands takes place, it is done in the same in that, the connection takes place in the superior and inferior series respectively. The interruption between the two series is retained throughout the petiole and rachis in the Cyatheeae, while in *Cibotium Barometz* it is limited to only a short distance, both series being connected in a single continuous band in the greater part of the leaf-axis. This is the greatest apparent difference in the petiolar bundles between the Cyatheeae and *Cibotium Barometz*.

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1) Bower, F. O. (1913) Ann. of Bot., Vol. 27.
2) Bower, F. O. (1921) Proc. Roy. Soc. Edinb., Vol. 41.

e. The Mode of Parting of Leaf-Traces

Leaf-traces in *Cibotium Barometz* are parted from the stem stele as a continuous band, which is divided into numerous separate strands in the base of the petiole, while those of the Cyatheeae are parted from the marginal part of the stele at the gap as separate strands. The outward curving of the stelar margin in the latter tribe is the preparation for the parting of leaf-traces, and it may be considered that leaf-traces are parted, at first, as a continuous band, which is then divided into separate strands. From this point of view, the marginal turning of both sides of the gap may be considered to be a part of the leaf-traces as in *Cibotium Barometz*; in the latter, however, the connecting part of the leaf-traces is not only the lateral sides, but also the whole sides of the gap.

In the parting of the leaf-trace of *Cibotium Barometz,* the appearance of the curved process toward the center of the trace is a very characteristic feature; this becomes the upper projecting strands in the petiole. Corresponding strands can be found in the leaf-traces of the Cyatheeae, in which, however, these strands are derived from medullary bundles. In the Cyatheeae, there is another series of internally projecting strands on the lateral sides, which are derived also from medullary bundles. In *Cibotium,* the laterally projecting strands corresponding to those of the Cyatheeae are not so prominent. It is the fusion of the medullary bundles which makes the internal projections prominent in the Cyatheeae, while in *Cibotium Barometz*, these projections have no relation to the medullary bundles.

f. The Pinna-Trace

Pinna-axes of *Cibotium Barometz* have a vascular system similar to that of the upper part of the rachis. This relation holds good in all species of the Cyatheaceae. Moreover, the pinna-traces are derived from the lateral corners of the superior and inferior series of the rachis-bundles. In *Cibotium Barometz,* two traces thus parted are jointed so as to form a wavy band, while in the Cyatheeae they are separated throughout the pinna-axis. In the latter tribe, however, there is a small strand in the branching region, which connects the pinna-traces of both series. The behavior of this connecting strand in this tribe is similar to the mode of fusion of both traces in *Cibotium Barometz.*

g. Histological Structure

The histological structure of the stele and the mechanical tissue at the stem surface of *Cibotium Barometz* is similar to that of the Cyatheeae. The presence of a layer of tangential cells in the outer part of the pholem is also the same. But, in *Cibotium Barometz* the sclerenchymatous sheath on both sides of the stelar ring and the mucilage sacs in the fundamental tissue are not found. In *Cibotium Barometz* there are filiform hairs, but scales, such as are always present in the Cyatheeae, are not found.

h. The Sporangium

Sori are borne within the bivalved parts of the margin of pinnules. The sporangium has a flattened ellipsoidal form and is provided with a long stalk. The annulus is incomplete, about one-fifth of the whole ring consisting of somewhat thin-walled stomium-cells, and the ring of the annulus is not interrupted by the stalk, that is, the stalk attaches to the lateral side of the ring (Fig. 58). The oblique position of the annulus shows the Cyatheacean character, and the presence of the stalk is one of the characteristics of the Dicksonieae.

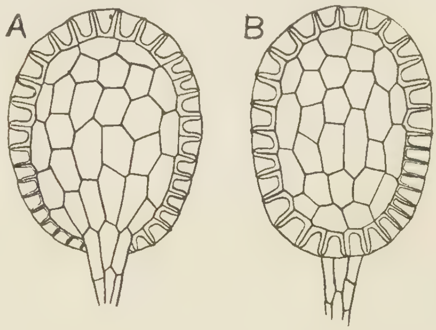

Fig. 58. Sporangia seen from two sides. (magnified)
A, Internal view
B, External view

i. Conclusion

In the characters above given, *Cibotium Barometz* differs from the other species of *Cibotium* in the absence of the sclerenchymatous sheath on the stelar ring, and in the creeping habit of the stem, while this species has internal characters and characterstic soral structure of the Cyatheaceae. The writer is not in the position to reach a final conclusion as to the affinity of the present species, until his knowledge of other species of this genus is more complete.

Summary

1. The stem of *Cibotium Barometz* is a creeping rhizome, which is covered with golden hairs. Leaves and roots are borne on the stem radially in spite of the creeping habit of the stem.

2. The stem is dictyostelic or solenostelic. The leaf-gap has not distinct boundary, as the leaf-trace is parted from the stele as a continuous band. Neither medullary nor cortical bundles are present.

3. The sclerenchymatous sheath on both sides of the stelar ring of the stem, which is one of the charaters of the Cyatheaceae, is not found in this plant.

4. A part of the stelar ring bulges out, and the separate leaf-traces are derived by a division of the part. The bulging part has a heart-shape in cross section, which is retained until after the division.

5. Root-traces are parted from the bulging part of the stele, or from the base of the parting leaf-traces.

6. At the base of the petiole, vascular strands are arranged in two series; the inferior series in a semicircular form at the lower side, and the superior series in a Γ7-shape, the arms of which are formed by the upper and lateral projections of the stelar margin at the gap.

7. The region of the petiole, where the vascular strands are found separate, is very short, and at the part a little above the base, they unite together into three wavy bands. The lateral interrupted part, that is, the limit of the superior and inferior series remains unconnected for a short distance, before it forms a single continuous vascular band. The last form is found up to the very top of the rachis. The limit of both series is marked by the lateral grooves.

8. When the pinna-trace is detached from the rachis-bundle, each lateral corner of the superior and inferior series of the latter elongates and gives off a small strand, and two strands thus parted connect in a continuous heart-shaped pinna-trace, which has the same form as the rachis-bundle.

9. Hairs on the stem and leaves are filiform, and are not scaly.

10. On the outer part of the stem is a hypodermal layer consisting of fibrous and parenchymatous cells. In the fundamental tissue, the fibrous tissue and mucilage sacs are not found.

11. The stele of the stem shows the normal fern-type in histological structure. On the outer side of the phloem is layer of tangential cells.

12. In the petiole, there is a thick hypodermis, and the fundamental tissue contains no mucilage sacs. The vascular strand has a normal structure of the fern-type.

13. Sori are borne within the bivalved indusia at the margin of the pinnules. The sporangium is stalked. The ring of the annulus is oblique, and contains stomium-cells to a certain extent.

14. Considering the above facts, *Cibotium Barometz* shows the general characters of the Cyatheaceae, but the absence of the sclerenchymatous sheath on the stem stele and the creeping habit of the stem are characters diverging from other species of the genus *Cibotium*.

VIII. Alsophilae from Formosa and the Loochoos*

Several species of *Alsophila* have been recorded from Formosa and the Loochoos, of which only three, viz. *Al. latebrosa*, *Al. podophylla* and *Al. formosana* are actually found[1]. In a trip to Formosa in July 1925 and to the Loochoos (Okinawa Island) and Ôshima in December 1925 and January 1926, the writer collected these three species. The following descriptions are based mainly on the material from Formosa, but partly on that from the Loochoos.

I. *Alsophila latebrosa*, Pr.

This is the largest and most common tree-fern in Formosa and the Loochoos, and has been identified with *Alsophila latebrosa*, which is further distributed in India and Malacca. Scott (1874) figured a part of the leaf, a cross section of the stem and petiole and other features of the same species based on material from British India. Judging from his figures, the writer is surprised to see that our plant from Formosa and the Loochoos is quite different in the structure of the stem and in the form of the leaf. If Scott's plant be truly *Al. latebrosa*, the Formosan plant appears to belong a different species. As the external features and internal structure of the stem and leaf of the Formosan plant almost coincide with those of *Alsophila Bongardiana*, these two plants may be considered to be in closest relationship. Having had no opportunity to examine *Al. latebrosa* from India or Malacca, the writer is not at present in a position to decide whether the identification of the Formosan species with the Indian is correct or not.

This Formosan species is found also in the Loochoos and Ôshima. The latter, situated at latitude 28° 20′ N. and longitude 129° 30′ E., seems to be the northern limit of its habitat.

The present study was mainly made with material collected near Taihoku, Formosa, that collected from Okinawa Island and Ôshima being used for comparison.

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* The contents of the Part VIII appeared in Japanese in the Bot. Mag. Tokyo, Vol. 40, pp. 401–417, July 1926.

1) Matsumura, J. et Hayata, B. (1906) Enumeratio Plantarum Formosanarum. Journ. Coll. Sci. Imp. Univ. Tokyo, Vol. 22; Hayata, B. (1916) Icones Plantarum Formosanarum, IV, Taihoku.

A. External Features of the Stem

The stem reaches a height of more than 10 meters, and bears characteristic leaf-scars on its surface. In a plant well grown, the lower part of the stem, up to about one meter in height above the ground, is covered with roots so densely that the stem itself cannot be seen; within the root-mass the stem tapers conically downwards. Above that part, the stem is cylindrical with a diameter of about 125 mm., and the leaf-scar shows an elliptical form with 65 and 44 mm. in longitudinal and transverse diameters respectively (Fig. 59, right). The scars shows a $\frac{3}{8}$ spiral arrangement, and two neighbouring scars on the vertical row leave a space just wide enough for a single scar. Proceeding upwards, the arrangement of scars undergoes a gradual change, and at the height of about 4 m. above the ground, it shows a quite different form. In this region, the stem has a diameter of 135 mm., and the leaf-scars, each circular in form, with an average diameter of 48 mm., are arranged in ten regular vertical rows (Fig. 59, left). This arrangement of scars in ten rows is derived from a $\frac{3}{8}$ arrangement, as in *Alsophila Bongardiana*. In other specimens, the scars are arranged in eleven to thirteen vertical rows, and are in contact with one another. The arrangement of vascular strands in the scar is according to the normal Cyatheacean type, and the projecting parts of the superior strands are so long that the strands at the ends of both arms come in contact with each other (Fig. 61).

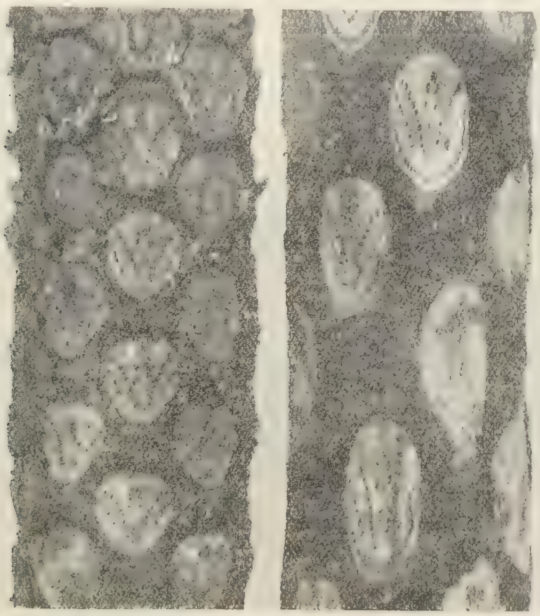

Fig. 59. *Al. latebrosa*; photograph of two parts of a stem, showing the change of the mode of arrangement of leaf-scars. ($\times \frac{1}{4}$)

Right, Lower part with a $\frac{3}{8}$ phyllotaxy
Left, Upper part with the scars arranged in ten vertical rows

The stem is covered with scaly hairs of a whitish or pale brownish

colour, but later they fall off, only those near the top of the stem remaining; in young plants and in those sheltered from the weather, they remain relatively longer.

B. Cross Sections of the Stem

The cross section of a stem at the basal part, having a $\frac{3}{8}$ phyllotaxy, has a circular outline, 120 mm. in diameter. The stelar ring, 92 mm. in diameter, lies within the periphery of the stem, and is interrupted by some leaf-gaps (Fig. 60, st). In a cross section, six gaps are usually found. On both outside and inside of the stele, a thick brown sclerenchymatous sheath is present (Fig. 60, sc). In the pith there are nearly 315 medullary bundles (Fig. 60, mb). The bundles situated at the

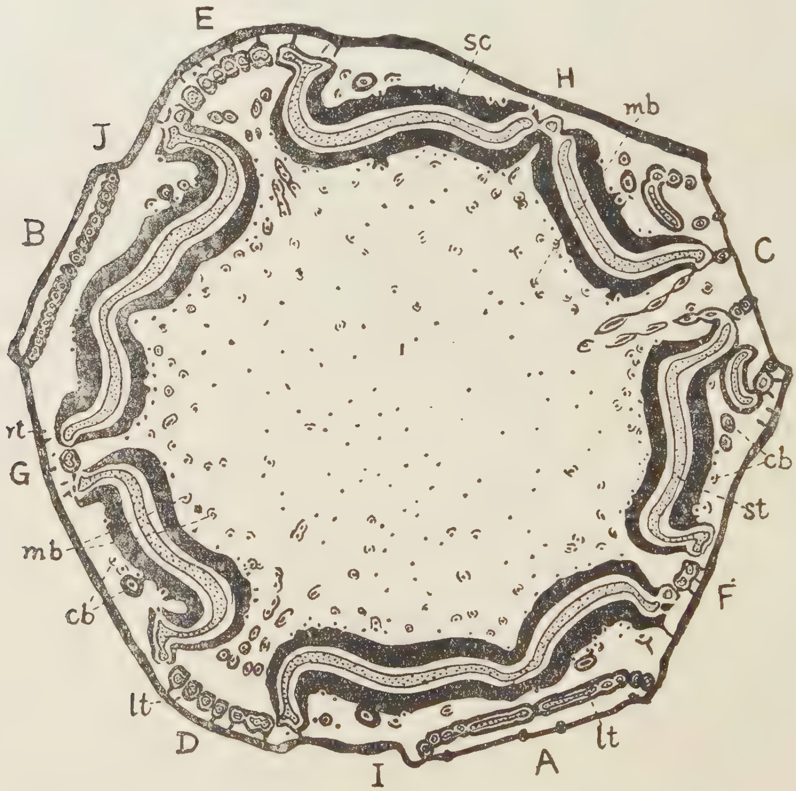

Fig. 60. *Al. latebrosa*; cross section of the stem. (×$\frac{4}{5}$)

A—J, position of leaf-gaps
sc, sclerenchymatous sheath
mb, medullary bundle
cb, cortical bundle
st, stele
lt, leaf-trace
rt, root-trace

periphery of the pith enter the grooves of the sclerenchymatous sheath, some of them occasionally being enclosed entirely within the sheath. Though some of the bundles are accompanied by their own sclerenchymatous tissue, most of them are not. The bundles with the sheaths are found near the leaf-gap. The sheath is not always of a complete ring-shape, but may form a discontinuous ring or even an arc.

In a cross section of the stem, cortical bundles are found usually numbering about 60, or 7–9 for each meristele (Fig. 60, cb). Most of them are in contact with the sclerenchymatous sheath of the stele, and enter its grooves slightly, just as do the medullary bundles, while some others are enclosed by distinct sclerenchymatous sheaths. The bundles of the latter type are found mostly near the leaf-gap.

In a cross section of a part of a stem, with a diameter of 120 mm., or with leaf-scars arranged in ten vertical rows, the gaps are seen to occupy ten regular positions, and each meristele tends to become semicircular owing to the closer approach of the gaps. The form of five gaps in alternate rows is similar, showing that five leaves of alternate rows are almost at the same level, as if they were in a whorl, as has been described in the case of *Alsophila Bongardiana*. The medullary bundles number 350, and the cortical ones 65, and both kinds, when situated near the sclerenchymatous sheath of the stele, enter deeply into the latter. The cross section of another stem, with a diameter of 85 mm., has a circular outline, and the stelar ring is divided by three or four gaps, which show a $\frac{3}{8}$ phyllotaxy. The outward curving of the meristelic margin at the leaf-gaps is relatively indistinct. About 120 medullary and 9 cortical bundles are found.

The largest stem observed by the writer has a diameter of 155 mm.

C. Solid Construction of the Stem

The solid construction of the stem, especially of the stelar system, was studied by comparing serial cross sections of a stem in the region with a $\frac{3}{8}$ phyllotaxy.

Here, the leaf-gap is twice as long as the corresponding leaf-scar. The marginal curving of the meristele at the gap recovers once at the upper part of the gap, and the leaf-traces parted from the upper and lower parts of this restricted region belong to the superior and inferior series of strands respectively.

Medullary bundles anastomose in the pith in a very complicated manner, and their upper ends communicate with the stelar margins at

the leaf-gap. The number of bundles belonging to a leaf-gap is not constant; there are usually five or six pairs. They always communicate with some leaf-traces belonging to the superior series. Usually, the first medullary bundle bifurcates a little before the fusion (Fig. 62, 1), and the inner branch enters the petiole directly, and becomes a strand situated at the very tip of the laterally projecting superior series (Figs. 61 & 62, f), while another branch fuses with the stele and forms a process, and the latter, being then separated as a leaf-trace, is situated next to the one derived from the first branch (Fig. 62, 2–4). In some cases, the first bundle fuses with the stele without bifurcating. Meanwhile, the original curved margin is separated successively as laterally projecting traces (Figs. 61 & 62, 3–5, d–e), and the new margin derived from the fusion of the medullary bundle curves outwards again, and successive leaf-traces branch off from the margin (Fig. 62, 4–6). The following medullary bundles fuse with the stelar margin at the gap, and produce some of the superior leaf-traces. Finally, two or three pairs of medullary bundles take a different course entering the petiole directly. In some cases, one of them bifurcates and both branches enter the petiole directly, or one of the branches enters the petiole and the other branch fuses to the stelar margin. In all cases, the last bundle or the last branch fuses with the stelar margin forming a process, producing the trace isolated at the upper median part (Figs. 61 & 62, 6–8, q). Though some bundles seem to enter the petiole directly, they also are branches of certain other bundles. Such is the case when the branching occurs at the lower level.

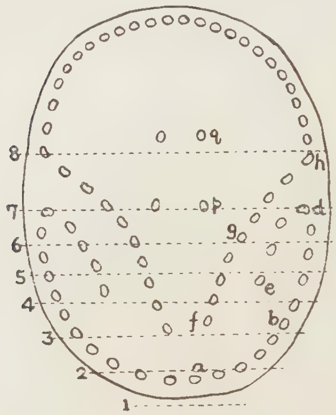

Fig. 61. *Al. latebrosa*; a leaf-scar showing the arrangement of vascular bundles; parallel lines (1–8) correspond to the levels of cross sections of Fig. 62; the lettering of the leaf-traces (a–q) corresponds to those of the same figure; c_1 and c_2 represent the cortical bundles. (nat. size)

Two pairs of cortical bundles belong to each gap (Fig. 62, c_1 c_2). At the level where two or three pairs of leaf-traces are parted from a gap, a pair of the cortical bundles near the gap becomes prominent, as each is enclosed in a sclerenchymatous sheath (Fig. 62, 1–3, c_1); then another pair takes the same course (Fig. 62, 1–3, c_2), and these two bundles

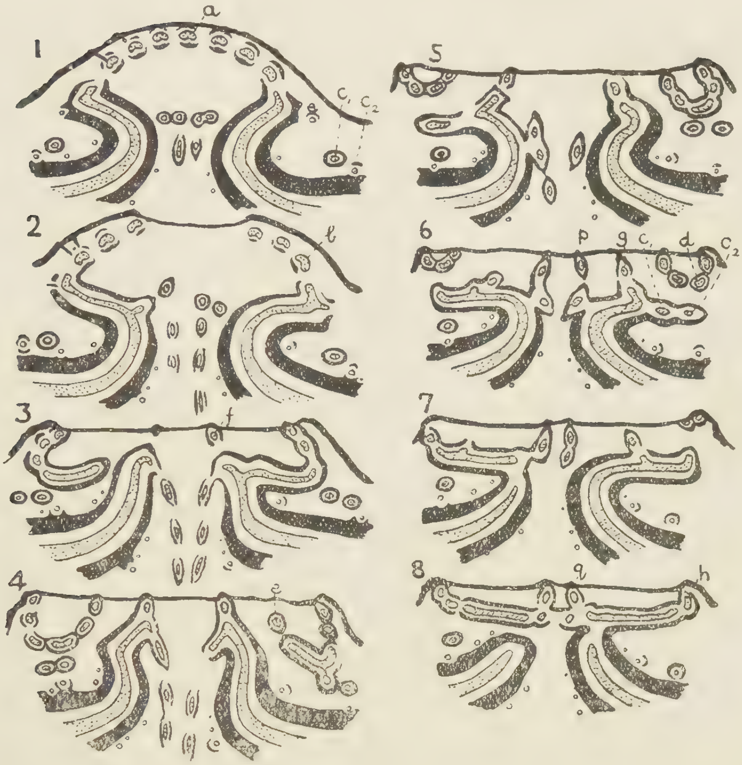

Fig. 62. *Al. latebrosa*; series of cross sections of a stem through a leaf-gap, showing the mode of parting of leaf-traces and the course of the medullary and cortical bundles. Sections in this figure correspond to the levels shown in Fig. 61, and the leaf-traces denoted by letters correspond to those shown in the same figure. (nat. size)

Explanations in text.

ascend side by side (Fig. 62, 2–5). At the level where the traces at the inferior lateral corner are given off, these two are enclosed in a common sheath (Fig. 62, 6), within which the two fuse into a single strand. Then, the fused bundle approaches the curved margin of the stele, and fuses there thus making the outward curving very prominent (Fig. 62, 7). The new margin thus formed is soon separated as a leaf-trace situated at the lateral corner of the superior series (Fig. 61 & 62, 8, h). In some cases, the cortical bundle fuses with the part belonging to the inferior strand temporarily, and separates again so as to fuse with the superior lateral corner.

D. Structure of the Leaf

The leaves are large consisting of muricated petioles and tripinnate

laminae. In a leaf of moderate size, the whole length reaching 2.5 m., a cross section of the petiolar base is semicircular, with transverse diameter measuring about 40 mm., or even 65 mm. in the largest specimens. Proceeding upwards, the outline becomes smaller and circular, until at the distal part of the petiole the diameter measures 20 mm.

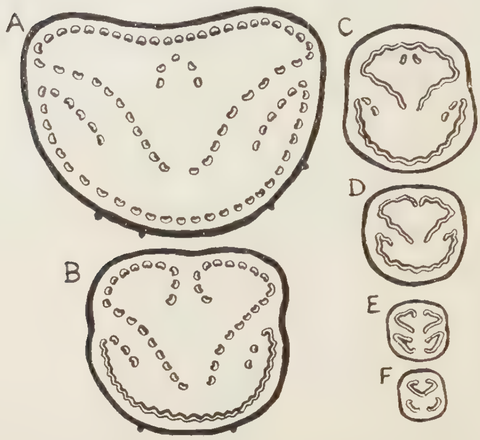

Fig. 63. *Al. latebrosa*; cross sections of different parts of a leaf-axis, showing the arrangement of vascular strands. (nat. size)

A, Extreme base of the petiole
B, Basal part of the petiole
C, Lower part of the petiole
D, Middle of the petiole
E, Top of the petiole
F, Middle of the rachis

The arrangement of vascular strands in the petiolar base shows the characteristic Cyatheacean type, as is seen in the leaf-scar (Fig. 63). At the petiolar base of a large leaf, with a lateral diameter of 40 mm., there are 47 pairs of strands (Fig. 63, A). Of the inferior 21 pairs, 16 pairs are arranged at the lower side in a semicircular form, and the other lateral 5 pairs project inwards, and out of the superior 26 pairs, 11 lateral pairs project deeply inwards, and 12 pairs form the upper sheet with a semicircular form, the other 3 pairs being isolated under the upper arc. The lateral projection of the superior series is prominent, two strands at the ends of both arms being close to each other.

Tracing the petiole upwards, we find that the strands connect with each other in a wavy form (Fig. 63, B). The arrangement of strands is not influenced by their connection, but the upper median part of the connected arc opens a little (Fig. 63, B). Then, the opening closes and the inner bundles become isolated (Fig. 63, C). Next, the arc opens again, and both margins thus formed join the internal isolated strands (Fig. 63, D). This three-banded formation is found at the middle or upper part of the petiole. At a part a little higher up, two superior bands connect to form a V-shaped band, while the inferior band is divided into two by the opening of the lower median part (Fig. 63, E–F). Still higher up, the inferior bands connect forming a single arc, and this shape may be maintained to the very tip of the rachis.

In the basal part of a pinna-axis, two to four vascular bands are arranged in the same way as in the upper part of the rachis. The mode

of branching of pinna-traces is of the so-called extra-marginal type, two traces being parted from the lateral corners of the rachis-bundles. A short commissure connects the two series at the branching region.

E. Structure of the Root

Roots part from the basal part of the petiole as is usual in the Cyatheaceae. In the region extending from the base to the height of 1 m. above the ground, they are especially abundant forming a thick mass around the stem. As the plant grows larger, the root-mass becomes correspondingly thicker. In one instance, the stem together with the enveloping root-mass measured 175 cm. in circumference, i. e. 56 cm. in average diameter, while the stem itself measured only 13 cm. in diameter. Roots are not borne on the higher part of the stem.

Root-traces are parted from the stelar margins at the lower half of the gap or from the bases of leaf-traces just given off.

F. Histological Structure

The tissue forming the outer layer of the stem usually falls off, but in small plants or in plants in sheltered positions, the surface is covered with scales. Under the epidermis, there is a parenchymatous layer, which is followed by a fairly thick sclerenchymatous layer. These layers are brownish in colour. When the external layer falls off, the external part of the parenchymatous layer is exposed. Between the internal fundamental tissue and the sclerenchymatous layer is interposed a layer of peculiar cubical cells. The sclerenchymatous sheath on both sides of the meristele is thick, about 3–4 mm., and is composed of typical sclerenchymatous fibers.

The meristele, with a thickness of 2–3 mm., is of the normal fern-type. The xylem consists of tracheids and parenchyma, and on the external surface of the phloem, is a layer of tangential cells. But, the presence of the latter is not constant, sometimes being replaced by a layer of mucilage cells, or longitudinally elongated cells. Sometimes, both kinds of cells are found in one and the same layer, so that the two kinds of cells, tangential and mucilage cells, may be of the same histological origin, the only difference being in their direction, either horizontal or vertical.

The fundamental tissue consists of whitish parenchyma, in which mucilage sacs are enclosed.

The medullary and cortical bundles have the same histological

structure; they are protostelic. The xylem in a small bundle consists of only a tracheidal mass, but in a larger one it contains a parenchymatous pith, and in the largest bundles a central cavity is found. The sclerenchymatous sheath which surrounds each bundle is composed of fibrous elements.

In the petiole and rachis, beneath the external parenchymatous layer, is a thick sclerenchymatous sheath, the fundamental tissue of which includes some mucilage sacs. The vascular strand is of normal construction, and at the inner median part of the curved xylem is the protoxylem, usually with a cavity. Surrounding the bundle, on the outside of the endodermal layer is a sclerenchymatous sheath.

The root is constructed according to the normal type, i. e. within a thick layer of the cortex is the central stele of a diarch form.

G. The Young Plant

The stem of the young plant tapers conically toward the lower tip, and on its surface numerous leaf-scars are seen. In order to ascertain the internal structure, the stem of a young plant with a constricted part was used for investigation. Serial cross sections at the basal part of this plant, as far as 130 mm. from the basal tip, were made. The general features in the main regions were as follows:

Region	A	B	C	D	E	F	G	H	I
Distance from the lower tip (mm.)	2	11	18	31	46	63	86	111	133
Diameter of the stem (mm.)	3	8	9	14	20	25	33	37	25
Diameter of the stele (mm.)	1	3	5	8	14	17	22	26	18
Number of leaf-gaps	1	1	2	3	2	3	3	4	4
Length of the leaf-gap (mm.)	–	3	4	7	10	11	16	15	15
Number of leaf-traces (in pairs)	1	2	3	4	7	10	12	14	14
Number of petiolar strands (in pairs)	1	2	4	6	9	12	14	17	17
Number of medullary bundles	0	3	9	16	33	36	50	89	86
Length of the medullary bundle (mm.)	–	4	7	13	–	–	–	–	–
Number of cortical bundles	0	0	0	0	0	0	3	6	7
Length of the cortical bundle (mm.)	–	–	–	–	–	–	15	24	15

The size of the stem and the stele increases gradually upwards to Region H, whence it decreases for a short distance. The size of the

leaf-gap also increases, and their arrangement is $\frac{2}{5}$ at the lower part, but changes gradually to $\frac{3}{8}$, and in the upper part of this material the phyllotaxy is intermediate between $\frac{2}{5}$ and $\frac{3}{8}$.

The number and mode of parting of the leaf-traces and the arrangement of petiolar bundles differ considerably at different levels of the stem. When the petiolar bundles are less than five pairs, they are arranged in a circle, but when they are six pairs one lateral pair of the superior series is situated slightly within the circle. In keeping with the increase of the bundles, the lateral projection becomes prominent, and in the case with nine pairs, the lateral two of five superior pairs project inwards, then also a lateral pair of the inferior series shows the same tendency. In the upper region (Region G), where there are fourteen pairs of petiolar bundles, the superior series consists of seven pairs, of which the lateral three and upper one project inwards, and of seven pairs of the inferior series, one lateral pair projects inwards. A little higher, one upper projected pair is found in an isolated state (Regions H–I).

The mode of parting of the leaf-traces is influenced by the fusion of the medullary and cortical bundles, but the course of these bundles is very complicated, even in the young part. This condition makes it impossible to trace them exactly. The appearance of the medullary bundle takes place very early (a little above Region A), when the diameter of the stele is about 1 mm. The first bundle which appears in the pith, ascends through the latter, and fuses with the meristele at the leaf-gap. The first three bundles fuse at one side of three gaps respectively, and the next ten bundles which appear also in the pith bifurcate, the two branches of each bundle fusing with the sides of the successive ten gaps. The stelar part connected by such a strand produces a leaf-trace corresponding to the last superior series. A little further upwards, the bundles which belong to a gap appear in pairs, and both bundles fuse with the stelar margins. But, sooner or later (in Region C), the mutual fusion of the bundles takes place, and the exact course of individual bundles cannot be traced completely. In Region D, a bundle which belongs to one side of a leaf-gap bifurcates just before ending, the former branch producing the first trace, and the last branch the last trace of the superior series. Their mutual connection is then complicated, and the number of branches which should be connected

with a leaf-gap becomes inconstant. When several pairs of them belong to a gap, the first pair produces the first pair of traces, the last pair the last, and the intermediate pairs the intermediate traces of the superior series.

The cortical bundle appears in Region G, i. e. far later than the medullary bundle. The bundles appear in pairs in the cortex, in contact with the outer surface of the sclerenchymatous sheath, and ascending through it connect with the stelar margins at the leaf-gap. Such a part is then separated as the leaf-trace situated at the lateral corner of the superior series. The bundles repeat this process regularly, and their length gradually increases.

Now, in the adult plant, there are two pairs of cortical bundles belonging to each gap, while in the young plant there is only one pair. Even in the material with a diameter of 80 mm. or more, there is but one pair of them, while some of the bundles bifurcate in their course, and these two are jointed into a strand again before they end. This may be the type transitional from the young to the adult form.

II. *Alsophila podophylla*, Hk.

The stem of *Alsophila podophylla* is erect and relatively small. Its usual height is 1–2 meters, but sometimes it grows as high as 3 meters. The bases of petioles, which are dark violet brown, are left on the stem, densely covering the latter. Roots are grown all around the stem, and cover its surface. The leaf is characterized by the bipinnate lamina.

This species is distributed widely in the South-West Islands of Japan, South China and Siam. Most of the material used was collected at Urai, near Taihoku, Formosa, but some came from Okinawa, one of the Loochoo Islands.

A. Cross Section of the Stem

A cross section of the stem is circular, except at points corresponding to the attachment of petioles, where projections give it the form of an irregular polygon (Fig. 64). Usually, the diameter of the stem is nearly 60 mm., that of the largest stem observed by the writer being about 90 mm. The stelar ring situated at the periphery of the stem is

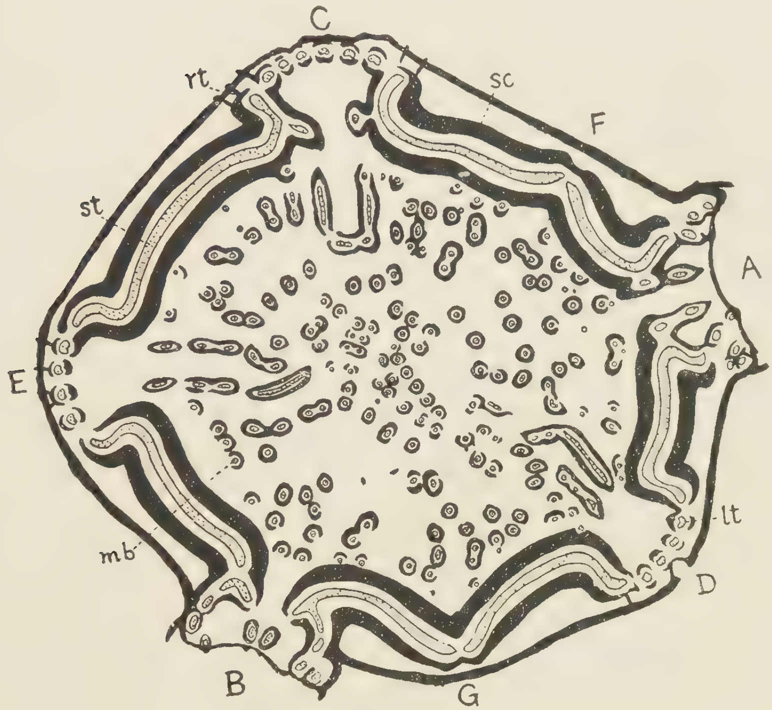

Fig. 64. *Al. podophylla*; cross section of the stem. (nat. size)
Abbreviations as in Fig. 60.

provided on both sides with sclerenchymatous sheath. Medullary bundles are very prominent, because of the presence of a very thick brown sheath enclosing each bundle (Fig. 64). Cortical bundles are not found.

The stelar ring is divided into six or seven meristeles, and the margins at the gap curve outwards, and give off leaf-traces and root-traces successively. The meristele, therefore, is arc-shaped, and is enclosed in a very thick sclerenchymatous sheath, the outline of which is not usually influenced by the medullary bundle.

The medullary bundles, 170–200 in number in a cross section, are distributed uniformly in the pith. Most of them are enclosed in distinct sheaths. The latter are usually ring-shaped, but in smaller bundles they are arc-shaped. Two or more bundles are occasionally enclosed in a common elliptical sheath (Fig. 64).

B. Solid Construction of the Stem

By comparing successive cross sections, the writer was able to see the solid construction of the stem, especially of the stelar system.

The stele of the stem is a hollow cylinder, the wall of which is perforated by numerous leaf-gaps which follow in $\frac{3}{8}$ phyllotaxy. The stelar margin at the gap curves outwards considerably, and from it the leaf-traces branch off successively. The entrance of the gap is fusiform with a longitudinal axis of about 30 mm., and the outward curving of the lateral margins recovers once near the upper end, so that the marginal curving is constricted; the leaf-traces which branch from the upper and lower parts of the constricted portion belong to the superior and inferior series respectively. There are about twenty pairs of vascular strands at the base of a petiole, and they are about equally divided into two series.

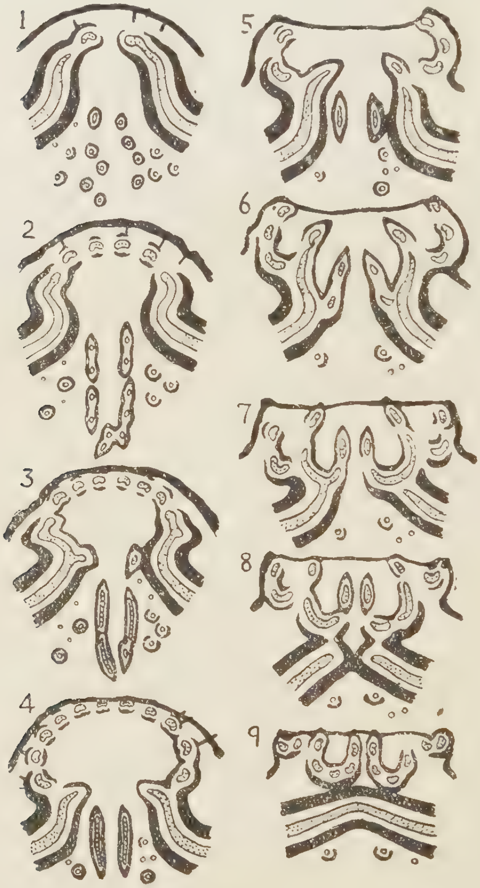

Fig. 65. *Al. podophylla*; series of cross sections of a stem through a leaf-gap, showing the mode of parting of leaf-traces, and the course of the medullary bundles. (nat. size)

Explanations in text.

The solid construction of a leaf-gap and the course of the medullary bundles will now be described, from cross sections made from below upwards (Fig. 65). The stelar ring bulges out at the lower part of the gap, and this finally opens (Fig. 65, 1). The gap broadens gradually, and at the same time, the margin curves outwards giving off successive leaf-traces (Fig. 65, 2–3). At the level where the leaf-traces reach as many as six or seven pairs, they are arranged in an arc, and some pairs of medullary bundles are arranged in two rows, two or three bundles being enclosed in a common sheath (Fig. 65, 3–4). Tracing these upwards, we see that the first pair of the medullary bundles fuses with the inner surface of the curved stelar margin, forming a process pointing inwards (Fig. 65, 3–4). At the same time,

the curved part of the original stelar margin is parted, and produces the laterally projecting leaf-traces of the inferior series (Fig. 65, 4–5). The process made by the fusion of the first medullary bundle becomes the new margin (Fig. 65, 4). Then, from this new margin leaf-traces corresponding to those at the lateral projection of the superior series are given off (Fig. 65, 5–6). The gap broadens gradually, and the margin curves again. Meanwhile, some of the medullary bundles at the leaf-gap are enclosed in a common sheath, within which they are fused into a strand (Fig. 65, 3–5), which in turn fuses with the inner face of the curved stele to form a process (Fig. 65, 6–7). This process and the curved stelar margin are then, as a whole, separated from the stele (Fig. 65, 7), and this part is divided into some leaf-traces situated at the upper sheet. Prior to the fusion of the last medullary bundle, it bifurcates, the outer one of the two going to the petiole directly without communicating with the stele (Fig. 65, 6–8), and situated in the petiole at the median upper part, it projects deeply inwards.

In short, though there are some pairs of medullary bundles in each leaf-gap, they are combined with each other, until at the upper part of the gap they fuse into two pairs. These two produce the first and last pairs of the superior leaf-traces, while a branch derived from the last pair directly enters into the petiole, in which it projects deeply in the median part.

C. Structure of the Leaf

The leaf is usually 2.5 m. in length, and the petiole is relatively short reaching from one-third to one-fourth of the whole length of the leaf. The petiole has numerous small spines on the lower side, especially at the basal part. Throughout the petiole and rachis, lenticels are arranged in a row on each lateral side.

A cross section of the petiole at its basal part has a semicircular outline flattened on the upper side. Petiolar strands are arranged in a peculiar manner (Fig. 66, A). In a petiole with a diameter of 23 mm., there are 22 pairs of strands, of which 12 pairs belong to the superior series, and the other 10 pairs to the inferior. Out of the latter strands, 8 pairs are arranged in a semicircular shape at the lower side, while the other 2 pairs project inwards. The superior strands are arranged

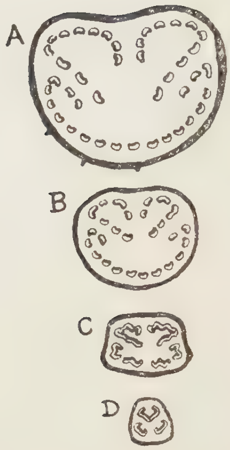

Fig. 66. *Al. podophylla*; cross sections of different parts of a leaf-axis, showing the arrangement of vascular strands.
(nat. size)
A, Base of the petiole
B, Middle of the petiole
C, Top of the petiole
D, Middle of the rachis

in a Γ7-form, the longer arm of which consists of 4 pairs corresponding to the lateral projection, and the other 8 pairs are situated at the upper side, while 1 or 2 pairs at the median part project somewhat inwards forming the short arm of the 7.

Tracing the petiole upwards, we see that the outline in cross section becomes circular, and vascular strands fuse to each other, so that in the upper part of the petiole, each of the superior and inferior strands becomes 7 pairs, arranged in the same way as those in the basal part (Fig. 66, B). Proceeding still further upwards, the neighbouring strands fuse together side by side in a wavy form, and at the middle part of the rachis, there are four such wavy bands, two superior and two inferior (Fig. 66, C-D). Further upwards, the long arms of the superior strands are connected so as to form a V-shaped superior band, and the inferior bands fuse also to form a curved band. This form with two bands of the vascular system is retained up to the summit of the rachis.

The mode of branching of pinna-traces from the rachis-bundle is of the so-called extra-marginal type. Two small strands which are constricted off from the corners of the superior and inferior series of the rachis-bundles enter the pinna-axis, in which they show an arrangement similar to that in the upper part of the rachis. In the branching part there is a small strand which connects the two traces.

D. Structure of the Root

The roots, which are adventitious, are borne all around the stem, and run down among the petiolar bases, covering the stem surface, as is usually the case in tree-ferns. Their course is influenced by the crowding of the petioles, so that they appear as if they were anastomosing with one another in an irregular manner. In this species, it is characteristic that several roots spring out of the petiolar remnant upwards as a small mass, and when they are long, they turn at first

upwards and then their terminal ends hang down. Some of the roots penetrate into the petiole through the half-decayed surface. The fundamental tissue of the petiole decays early, but the external hypodermal layer persists for a long time, the layer on the outer side of the petiole being resisted to decay than that of the inner wall. Thus, the roots which penetrate into the petiole through the inner wall cannot always penetrate the outer wall of the petiole, so that they go downwards into the fundamental tissue of the petiole, or else are obliged to turn upwards, until they emerge out of the petiole. This course of the root, therefore, has nothing to do with its negative geotropism.

E. Histological Structure

The histological structure of the stem of this species is of the normal Cyatheacean type, and needs no further explanation. The most characteristic feature of this species is the development of the sclerenchymatous tissue to form the hypodermal layer, the sheath on both sides of the stele and also the sheath of each medullary bundle. In a plant of moderate growth, the hypodermis measures about 1 mm. in thickness, of which the outer half consists of parenchyma and the inner half of sclerenchyma. The meristele has an average thickness of 2 mm., and the sclerenchymatous sheath which surrounds it is as thick as 2–3 mm. The meristele consists of the central xylem and the phloem on both sides, and on the external part of the latter there is a layer of tangential cells. Mucilage sacs are found in the fundamental tissue. At the boundary between the sclerenchyma and fundamental tissue there is a peculiar layer consisting of cubical cells. The medullary bundle is protostelic consisting of the central xylem and the surrounding phloem-layer. In the smaller ones, the xylem consists of a tracheidal mass, but in the larger it contains a parenchymatous pith.

Under the thin subepidermal parenchymatous layer of the petiole, is a sclerenchymatous hypodermal sheath. The separate bundle in cross section has a form somewhat curved, and is surrounded by a layer of fibers. The xylem is arc-shaped, and at the median inner side there is a protoxylem with a cavity. The phloem surrounds the xylem, and is much thicker on the inner side of the xylem-arc than on the outer side.

The root structure is of the normal fern-type; surrounded by a thick cortex, the stele has a diarch bundle.

F. The Young Plant

The young plant of this species tapers toward the lower tip conically, and is covered with petiolar bases. Serial cross sections of a young stem through a length of 60 mm. were made, and by a comparison of them the solid construction of the stem was studied.

In the first place, the size of the stem and stele, the number of leaf-traces, the number and length of the medullary bundles, etc. in six main regions will be shown in the following table:

Region	A	B	C	D	E	F
Distance from the lower tip (mm.)	1	3	6	13	21	40
Diameter of the stem (mm.)	4	7	10	19	20	40
Diameter of the stele (mm.)	2	4	6	11	10	17
Number of leaf-gaps	2	3	3	3	4	4
Length of the leaf-gap (mm.)	–	1	3	6	9	11
Number of leaf-traces (in pairs)	1	1	2	2	3	5
Number of petiolar strands (in pairs)	1	1	2	3	4	7
Number of medullary bundles	0	0	5	12	22	46
Length of the medullary bundle (mm.)	–	–	3	6	10	25

The increase in size of the stem and stele from the tip upwards is gradual. The size of the leaf-gaps increases in the same way, and their arrangement, i. e. the phyllotaxy is $\frac{2}{5}$ at the basal part, and changes gradually to $\frac{3}{8}$ toward the stem apex. Leaf-traces are given off in succession from both margins of the leaf-gap, and some of them are divided in their course, so that the petiolar bundles become more numerous than the parted leaf-traces. In a petiole with three pairs of vascular strands, they are arranged in a circular form, but in one with more than four pairs of strands, at least one pair on the lateral side projects inwards.

The medullary bundle makes its appearance a little below Region C, or near the tenth leaf-gap. Proceeding upwards, the number of bundles increases gradually. The bundles which belong to each gap are usually one pair, which appears in the pith below the corresponding gap, and ascending through the pith fuses with the stelar margin, the fused part being parted as the last or upper median leaf-trace. A little higher up (Region E), the medullary bundle bifurcates a little before fusing; one of the branches continues the same course as in the former case, while the other branch fuses with the lateral side of the stelar

margin, and produces the first strand of the superior series. Irregularities are sometimes met with, e. g. in some cases, a medullary bundle bifurcates but the two branches fuse into one before ending, and in another case, two strands which appear in the pith fuse into one.

The sclerenchymatous sheath surrounding the medullary bundle is very prominent even in the young plant. It appears in company with the bundle, but sometimes the sheath-tissue appears before the bundle itself, so that isolated sclerenchymatous masses are often found in the pith.

G. Adventitious Buds

In a stem with a diameter of about 50 mm., numerous adventitious buds in groups were found, the one group consisting of six buds and

Fig. 67. *Al. podophylla*; a sketch of a part of the stem with adventitious buds. ($\times\frac{3}{4}$)

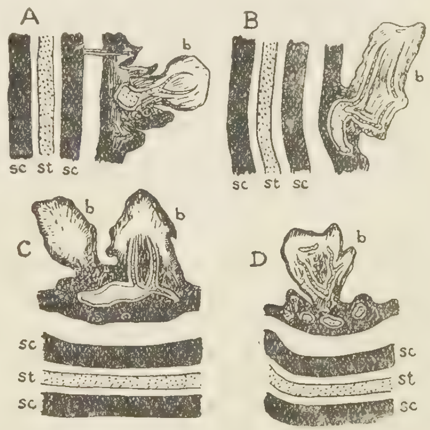

Fig. 68. *Al. podophylla*; sections of the stem with adventitious buds. (nat. size)
A & B, Radial longitudinal sections
C & D, Transverse sections
st, stele b, bud
sc, sclerenchymatous sheath

the other of three (Fig. 67). The buds are small in size, usually 5–15 mm. in length, and even in the largest the length is only 30 mm. The bud tapers toward the base and broadens upwards conically, as in the young plant. It is covered with remains of petioles, and living leaves, which reach a length of 10–20 cm., are found only at the apical region of the bud.

It is very remarkable that the vascular system of the bud has no connection with that of the stem. Involved within the brown hypodermal layer of the stem, is an irregular mass of vascular tissue, a part

of which elongates outwards into the bud, and constitutes the vascular system of the latter (Fig. 68). This irregular mass of vascular tissue in the hypodermis may be completely included within it, or may extend somewhat to the outer part of the fundamental tissue; but in no case does it communicate with the stem stele itself. Such independence of the vascular system of the stem and of the bud is very peculiar, and the writer thought, at first, that spores might have germinated on the stem and developing buds penetrated into the stem tissue. But, at the boundary between the irregular stelar tissue of the bud and the surrounding tissue of the stem, there are no indications of their being crushed or disturbed.

The bud has a diameter of 3 mm. at its base, and the stele within it shows a protostelic or solenostelic structure. In the latter case, the stele has a brown sclerenchymatous mass in the center. Upwards, we see that the solenostele becomes larger, and a part projects so as to give off a pair of leaf-traces, and through the leaf-gap the sclerenchymatous sheaths on both sides of the stelar ring are connected.

The sclerenchymatous tissue on the outside of the stelar ring appears, at first, in irregular masses along the stelar ring, and these gradually come together so as to form a continuous ring. The internal sheath, which appears in the pith as a mass, increases, and when the external sheath closes into a ring, the internal mass is made a ring-shape by the appearance of the central parenchyma.

III. *Alsophila formosana*, Bak.

The stem of *Alsophila formosana* is represented by a creeping rhizome which tapers toward the basal tip conically. It attains a length of 15 cm. In a well grown plant, the diameter near the top reaches an average length of 35 mm. Leaves and roots are borne on the stem radially, thus giving the stem a dorsiventral appearance. In general features, therefore, it resembles *Alsophila acaulis*.

This species is believed to be endemic to Formosa. The material used was collected at Sôzan, near Taihoku, Formosa. The writer collected this plant also in the Okinawa and Ôshima Islands.

A. Cross Section of the Stem

A stem of a moderate size generally exhibits a triangular shape in cross section owing to the attachment of petioles (Fig. 69). Its average

diameter reaches 35 mm. The stelar ring, whose average diameter is 23 mm., has generally three gaps, where the stelar margins elongate outwards and give off leaf-traces. From the relative position of the gaps, the phyllotaxy is easily seen as nearly $\frac{2}{5}$. The meristele is relatively thin, and provided externally and internally with sclerenchymatous sheaths.

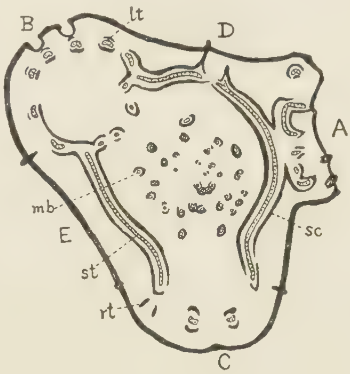

Fig. 69. *Al. formosana*; cross section of the stem. (nat. size) Abbreviations as in Fig. 60.

In the pith, thirty-five medullary bundles are found in a cross section, and nearly all of them are enclosed in brown sclerenchymatous sheaths. The sheath is usually of an irregular arc-shape, but in rare cases is ring-shaped. The bundles are numerous in the central part of the pith. Some of the bundles are in contact with each other; in such a case, the sheaths which surround two or more bundles connect so as to form the irregularly connected common sheath, which is one of the characteristics of this species.

B. Solid Construction of the Stem

Though the stem is prostrate, exhibiting a dorsiventral appearance, the attaching points of leaves are in a regular radial position following a $\frac{2}{5}$ phyllotaxy, which is most clearly seen by the relative positions of leaf-gaps on the stelar ring. The leaf-gap is fusiform, about 10 mm. in length, its marginal parts turning outwards.

Two pairs of medullary bundles belong to each leaf-gap, and are connected with the first and the last pairs of superior leaf-traces. The attaching point of the first bundle corresponds to the recovering part of the outward curving of the stelar margin. Tracing the medullary bundles downwards, they are connected with each other in their course, but finally end blindly in the pith.

C. Structure of the Leaf

The leaf reaches a length of 2 m., of which the lower half or two-thirds is the petiole, the lamina being of relatively small size. The

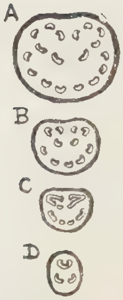

Fig. 70. *Al. formosana*; cross sections of different parts of a leaf-axis, showing the arrangement of vascular strands. (nat. size)
A, Base of the petiole
B, Middle of the petiole
C, Top of the petiole
D, Middle of the rachis

cross section of the petiolar base is nearly circular, though the upper side is somewhat flattened. There are nine pairs of vascular strands arranged in the Cyatheacean type (Fig. 70, A). Of these, four pairs belong to the inferior series arranged on the lower side semicircularly, while the other five pairs of the superior series are arranged in a ⌈7-shape, the longer arm of which consists of two strands projecting laterally, and the shorter arm of one strand. Tracing the petiole upwards, we find that the number of strands decreases gradually by the fusion of adjacent strands, until at the middle part of the petiole, three pairs are found in each series (Fig. 70, B). Higher up, the strands connect in four wavy bands, and at last, the two superior bands connect in a V-shaped band, and the two inferior also fuse into one (Fig. 70, C–D).

The branching of pinna-traces takes place after an extra-marginal type, that is, they branch from the lateral corners of the superior and inferior series of the rachis-bundles, and are connected temporarily by a short commissural strand.

D. Histological Structure

The stem and leaf exhibit the normal Cyatheacean type in histological structure, but as they are of small size, the structure is simple as in *Alsophila acaulis*.

The outside of the stem is brown covered with scaly hairs, and in the subepidermal part there is a sclerenchymatous layer consisting of fibers. The sclerenchymatous sheath on both sides of the stelar ring consists of typical fibers, marked off from the fundamental tissue by a layer of cubical cells. The stelar ring is relatively thin, and on the external side of the phloem is a layer of tangential cells. The medullary bundle is constructed in a characteristic manner. Its xylem consists of a tracheidal mass, with or without parenchymatous cells. The sclerenchymatous sheath which surrounds the bundle has a very irregular outline. In the fundamental tissue of the stem mucilage sacs are found.

Beneath the epidermis of the petiole and rachis, there is a thick hypodermal layer of fibers. Each of the separate bundles has a semi-

circular outline. On the inner side of the xylem, is a protoxylem with an indistinct cavity. In the fundamental tissue some mucilage sacs are found.

The root has a thick cortex, brown in colour, and the stele has a diarch bundle.

E. The Young Plant

The basal tip of the stem of the young plant tapers conically, and remains of petioles cover the stem. The attachment of leaves is radial, though the stem is creeping. The stem is usually triangular in cross section, due to the attachment of petioles, the outline of the stelar ring following the stem outline.

In order to ascertain the solid construction of the basal part of the stem, successive cross sections of a young plant were made, through a length of 60 mm. from the tip. The numerical relation of each tissue in six main regions will be given below:

Region	A	B	C	D	E	F
Distance from the basal tip (mm.)	2	7	15	24	37	56
Diameter of the stem (mm.)	4	9	10	18	22	27
Diameter of the stele (mm.)	2	4	6	10	12	15
Number of leaf-gaps	3	3	3	3	3	4
Length of the leaf-gap (mm.)	–	4	8	10	12	15
Number of leaf-traces (in pairs)	1	2	3	3	4	5
Number of petiolar strands (in pairs)	1	2	3	3–4	5	6
Number of medullary bundles	0	0	5	13	17	22
Length of the medullary bundle (mm.)	–	–	–	11	15	20

The increase in size of the stem and stele is gradual, and their diagram of development shows a regular parabolic shape. The size of the leaf-gaps also increases gradually, and their arrangement, i. e. the phyllotaxy, is not affected by the dorsiventrality of the stem; it is $\frac{2}{5}$ at the base but has a tendency to change to $\frac{3}{8}$ toward the top. Three gaps usually overlap in a cross section.

Leaf-traces are few in number even in the adult plant, so that in the younger part they are only one to five pairs in each leaf-gap, of which the last pair usually bifurcates in the cortex of the stem, so that the vascular strands at the basal part of the petiole are more numerous than the leaf-traces parted from the corresponding gap. In the petiole,

when the strands are less than three pairs, they are arranged in a circular form, but when there are more than three pairs, the lateral pair is so situated as to project somewhat inwards.

Though the medullary bundles sometimes take an irregular course, most of them follow a general type. They appear in the pith, and connect with the stelar margin at the gap, the connecting part being separated as a leaf-trace situated at the upper median part of the petiole. The first appearance of the bundles takes place in pairs at a level a little below Region C. A pair of the bundles, which appears near the gap, ascends through the pith, and fuses with the stelar margin of the leaf-gap. Somewhat higher, the medullary bundle bifurcates, and the two branches fuse again into one, which connects with the stelar margin. Proceeding still higher upwards, the bifurcated strands fuse with the stele separately, one producing the first and the other the last leaf-trace of the superior series. In some cases, irregularities take place, e. g. two or three bundles combine into a single strand, or one bundle bifurcates. The length of the medullary bundles themselves increases in keeping with that of the gap; it is usually twice as long as that of the corresponding gap.

F. Adventitious Buds

On the stem of this species adventitious buds are often found. In one plant two buds were borne. They are small and bear some leaves at the top. The stelar system of the bud has no direct connection with that of the stem, and the basal part of the bud stele is seated in the outer cortex of the stem, forming an irregular mass. The stele of the bud is a typical solenostele at the basal part. In general features, the bud is quite similar to that of *Alsophila podophylla*.

Summary

1. *Alsophila latebrosa* is similar to *Al. Bongardiana* in such external features as the larger size of the stem, the leaf-scars on the stem surface, the form of leaves, etc., and also in such internal features as the structure of the leaf-gap, the presence of cortical bundles, etc.

2. The difference between *Al. latebrosa* and *Al. Bongardiana*, with regard to internal structure, lies in (a) that in *Al. latebrosa* the sclerenchymatous sheath surrounding the medullary bundle is found in the bundles situated at the periphery of the pith, while in *Al. Bongardiana* it is only in those near the leaf-gap, (b) that in *Al. latebrosa* there are

two pairs of cortical bundles in each leaf-gap, while in *Al. Bongardiana* only one pair, and (c) that at the base of the petiole of *Al. latebrosa* the vascular strands at the lateral projections are nearly in contact with each other, while in *Al. Bongardiana* they are separated. These differences are, however, not absolute, and in some cases it is found difficult or even impossible to make them distinctions.

3. *Alsophila podophylla* is similar to *Al. Ogurae* in such external features as the moderate size of the stem, the remains of petiolar bases on the stem, the dark violet-brown colouring of the petioles, etc., and also in such internal features as the structure of the leaf-gap, the mode of parting of leaf-traces, the course of medullary bundles, the arrangement of vascular strands in the petiole, etc.

4. *Al. podophylla* differs from *Al. Ogurae,* in internal structure, in that the sclerenchymatous sheath surrounding the meristele and medullary bundles is very thick and prominent.

5. *Alsophila formosana* is similar to *Al. acaulis* in such external features as the creeping habit of the stem, the smaller size of the leaves, the dark violet-brown colouring of the petioles, etc., and also in such internal features as the structure of the leaf-gap, the mode of parting of leaf-traces, the course of medullary bundles, the arrangement of vascular bundles in the petiole, etc.

6. *Al. formosana* differs from *Al. acaulis,* in internal structure, in that the sclerenchymatous sheath surrounding the medullary bundle shows an irregular outline, while in the latter species it is almost circular.

7. In external features as well as in internal structure, *Al. latebrosa, Al. podophylla* and *Al. formosana* are similar to *Al. Bongardiana, Al. Ogurae* and *Al. acaulis* respectively, showing a close affinity between each two species.

8. The histological structure of the vegetative organs in the three present species is of the normal Cyatheacean type. 'Tangential cells' and 'mucilage cells' on the outside of the phloem are of the same kind of tissue, the only difference lying in the different orientations of the cells.

9. In *Al. podophylla* and *Al. formosana,* adventitious buds are found on the stem. The vascular system of the bud has no connection with the stem stele.

IX. General Summary

From the observations on the structure of Japanese Cyatheaceae recorded above, the writer has reached the following conclusions. As the species thus far studied are comparatively few, a general conclusion based on the structure of all species of the Cyatheaceae cannot be given, but it seems possible, notwithstanding, to form a general conception of the structure of the family.

A. Systematic Review

In Japan the following species of Cyatheaceae have been found.

Scientific Names and Synonyms	Japanese Names	Distribution	
		In Japan	Elsewhere
Cyathea spinulosa WALL.*	Hego	Bonins, Kiushiu, Loochoos, Formosa	South China, Malacca, India
Alsophila acaulis, MAK.*	Kusa-maruhachi	Shikoku (Endemic)	
Al. Bongardiana, METT.* *Cyathea Mertensiana*, BONG.	Maruhachi	Bonins (Endemic)	
Al. contaminans, WALL.	Buchi-hego	Formosa	Trop. Asia
Al. denticulata, BAK. *Dryopteris denticulata*, HAY.	Nokogiriba-hego	Formosa(Endemic)	
Al. Fauriei, CHR.	Fumoto-hego	Loochoos(Endemic)	
Al. formosana, BAK.*	Chabo-hego Yambaru-hego	Formosa, Loochoos (Endemic)	
Al. latebrosa, PR.* *Hemitelia latebrosa*, METT.	Hikage-hego	Formosa, Loochoos	Malacca, India
Al. Ogurae, HAY.*	Me-hego	Bonins (Endemic)	
Al. podophylla, HK.*	Oni-hego Kuro-hego	Formosa, Loochoos	China, Siam
Al. pustulosa, CHR.	Hiyoke-hego	Loochoos(Endemic)	
Al. subglandulosa, HANCE *Dryopteris subglandulosa*, HAY.	Nebari-hego Missen-hego	Formosa(Endemic)	
Al. tomentosa, HK.	Aya-hego	Formosa	Celebes, Java
Al. truncata, BRACK.	Me-hego	Bonins	Celebes, Java
Hemitelia boninsimensis, DIELS *Alsophila boninsimensis*, CHR.	Shima-hego	Bonins (Endemic)	
Cibotium Barometz, SM.* *Cib. assamicum*, HK. *Cib. glaucum*, SM.	Takawarabi	Formosa, Bonins, Loochoos	Malacca, China
Dicksonia Smithii, HK. *Dennstaedtia Smithii*, MOORE	Taiwan-taka-warabi	Formosa	Philippines
Balantium formosae, CHR. *Dennstaedtia formosae*, CHR.	Taiwan-kaguma	Formosa(Endemic)	

* denotes the species described in this paper.

Cyathea spinulosa, the only species of *Cyathea* in Japan, is distributed widely in tropical Asia. Considered from the internal structure of the stem, it may be divided into four different types, which have been described as the Hachijô-, Bonin-, Loochoo- and Formosa-types. The internal structure of the stem of these four types shows quite different features, though the outward forms of the stem and the leaves seem to be identical. As there are also some intermediate or transitional types between them, these four types may be of one kinship. Thus, *Cyathea spinulosa* may be regarded as a variable species.

Although more than ten species of *Alsophila* have been described as found in Japan, about half of them are doubtful, so that there seem really to exist only five or six species. True specimens of the doubtful species have not been collected by the writer nor by many other botanists[1]. Among the species actually known, *Al. acaulis* and *Al. formosana* have creeping rhizomes and small leaves as their characteristics; these two species are similar in their general features. *Al. Ogurae* and *Al. podophylla* also are similar in general features, the stem being about 2 m. in height. *Al. Bongardiana* and *Al. latebrosa* have large stems reaching more than 10 m. in height, and their leaves fall clear from their very bases, leaving the characteristic scars on the stem surface. *Al. latebrosa* from Formosa and the Loochoos has been identified with *Al. latebrosa* from India, but this identification is doubtful (VIII, p. 280). The Formosan and Loochooan species is rather similar to *Al. Bongardiana*, so that the two must be closely related species.

Other species of *Alsophila* hitherto described were not collected by the writer. *Al. contaminans* and *Al. tomentosa*, which are common in tropical Asia, have been reported from Formosa, but it seems that some specimens of *Al. latebrosa* were incorrectly identified with these species. The case of *Al. pustulosa* from the Loochoos may be similar. *Al. truncata* was reported from the Bonins, but it is also doubtful. *Al. subglandulosa* and *Al. denticulata* are characterized by their inferior height, and have been thought by Dr. HAYATA to be species belonging to *Dryopteris*, but their existence is still doubtful.

Concerning the genus *Hemitelia*, its one species, *Hem. boninsimensis*, was reported from the Bonins. The writer has examined a fragment of the original specimen preserved in the Berlin-Dahlem Museum, which has a distinct indusium and is very similar to *Cyathea spinulosa*.

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1) HAYATA, B. (1916) Icones Plantarum Formosanarum. IV, p. 155.

Of the genus *Cibotium*, there is a species, *Cib. Barometz*, with a creeping rhizome, but its existence in the Bonins is doubtful.

As of the genera *Dicksonia* and *Balantium*, *D. Smithii* and *B. formosae* were described. Many species of these genera are to be included in the Polypodiacean genus *Dennstaedtia*, and so, in the case of the present species, they may be properly classified as belonging to the latter genus and not to the Cyatheaceae.

Thus, although more than eighteen species of Japanese Cyatheaceae have been described or reported, those that truly exist are apparently only eight. The reason for the larger number probably lay in the incompleteness of specimens and in undue haste in determination. The determination of ferns is usually based on the form of the leaves, but in the leaves of Cyatheaceae the form varies according to age, and differs even in different parts of the same leaf. The description of the Cyatheacean species is limited to only one part of the leaf, and determination by such an imperfect description may lead to an erroneous conclusion. The existence of species once described but not again actually found, may rest only on such carelessness. It is necessary to emphasize here, that in the description of the Cyatheacean species, the form of whole leaves, both young and adult, the character of stems, and, if possible, also the internal structure must be carefully considered.

B. Structural Characters and Their Application to Taxonomy

In the plant-kingdom, a systematical group or family, the classification of which is based upon external characters, has often special characters in its internal structure. In ferns this tendency is quite remarkable, each family having its own special structural character. In some families, the genera, or even the sections of a genus can be distinguished clearly by their internal structure. In the Cyatheaceae, most of the species have large leaves and stems, and can be distinguished from other fern-families at a glance. But, in the young plants or those with small stems, it is often difficult to determine, whether they should be included in this family or not. The vegetative organs of this family, however, have special structural characters, which are so definite that the family can be easily distinguished from others, even in very young plants.

The structural characters of this family are as follows; (1) the stem stele is dictyostelic, the stelar margin at the gap showing the

characteristic outward curving; (2) surrounding the meristele, there is a brown sclerenchymatous sheath; (3) the stem in most of the species is provided with medullary bundles, and in some cases with cortical ones as well; and (4) vascular strands in the petiole show the characteristic arrangement.

The Cyatheaceae are classified into three tribes based on the external features (I, p. 141). These tribes may be distinguished also by the characters of their internal structures, as shown below:

A. The stem has a polycyclic dictyostele, but the sclerenchymatous sheath and cortical bundles are absent. The petiolar bundle consists of a continuous wavy band . . . . Thyrsopterideae

B. The stem has a dictyostele provided with the sclerenchymatous sheath. Medullary and cortical bundles are wanting. The petiolar bundle consists of a continuous wavy band. . . . . . . Dicksonieae

C. The stem has a dictyostele provided with the sclerenchymatous sheath. Medullary bundles, and, in some cases, also cortical bundles are present. The petiolar bundle consists of numerous separate strands having the characteristic arrangement. . . . . Cyatheeae

Let us now consider the specific difference in respect of internal structure. Of the Dicksonieae, the only one species, *Cibotium Barometz*, has been observed, so that the comparison of the species of this tribe is impossible. Of the Cyatheeae, the species show different types in their internal structure according to the size or the age of the individuals even in the same species. The size and shape of the stele or meristele, the number and form of the leaf-gaps, the thickness of the sclerenchymatous sheaths, the number of cortical and medullary bundles, the number and arrangement of petiolar bundles, etc. are variable in different parts of one and the same plant, so that these characters cannot be used as standards for specific determination. The most useful standard for this purpose is the following, which may be applied to a cross section of any part of the stem; (1) the presence or absence of cortical bundle; (2) the presence or absence of denticular formation of the outline of the sclerenchymatous sheaths of the meristele; and (3) the presence or absence, and the form of the sclerenchymatous sheaths surrounding the medullary and cortical bundles.

The species which have been observed by the writer constitute only a part of this tribe, and it is uncertain whether these standards can be applied to all of the species. But, at least so far as the Japanese species are concerned, these standards can be constantly applied. The distribution of medullary bundles and the accompanying sclerenchymatous

sheaths are the most constant features and the most important factors in specific determination, so that in material which is devoid of the pith, or in dried specimens, the determination is difficult.

The following table is given as the key for the specific determination of Japanese Cyatheeae, from the point of view of internal structure, in a cross sectios of the stem.

I. In the stem there are medullary bundles but no cortical ones (Cyathean dictyostele; II, p. 202).
  A. Half of the medullary bundles have sclerenchymatous sheaths.
    a. Sclerenchymatous sheaths of medullary bundles are not of a ring-shape, but of a discontinuous arc-shape.
      1. The meristele curves in a shallow wavy form.
        α. The outline of the sheaths of the stelar ring is smooth. *Cya. spinulosa* (Hachijô-type)
        β. The outline of the sheaths of the stelar ring shows the denticulation. . . . . *Cya. spinulosa* (Loochoo-type)
      2. The meristele curves deeply in a horseshoe-shape. . . . . *Cya. spinulosa* (Formosa-type)
    b. Most of the sclerenchymatous sheaths of medullary bundles are ring-shaped. . . . . *Al. Ogurae*
  B. Most of the medullary bundles have sclerenchymatous sheaths.
    a. The sheath is of an incomplete ring-shape. . . . . . . *Al. formosana*
    b. The sheath is distinct and generally ring-shaped.
      1. The sheath is thin. . . . . *Al. acaulis*
      2. The sheath is thick and very distinct. . . . . *Al. podophylla*
II. In the stem there are medullary and cortical bundles (Alsophilan dictyostele; V, p. 260).
  A. Cortical bundles lack the sclerenchymatous sheaths. . . . . *Cya. spinulosa* (Bonin-type)
  B. Cortical bundles have the sclerenchymatous sheaths.
    a. Cortical bundles, two pairs in each gap. . . . . *Al. latebrosa*
    b. Cortical bundles, one pair in each gap. . . . . *Al. Bongardiana*

C. Erect and Creeping Habits of the Stem

The erect and creeping habits of the stem of the Cyatheaceae have been discussed in the case of *Alsophila acaulis* (IV, p. 234), and it is not necessary to repeat here. With some additional observations, the writer's conclusions on this point may be stated briefly.

The writer has observed three species which have creeping rhizomes :—*Alsophila acaulis*, *Al. formosana* and *Cibotium Barometz*.

The genus *Alsophila* includes more than one hundred species, or about half of all the Cyatheaceae. In the species belonging to this genus, only one species, *Al. blechnoides*, was known to have the creeping stem, which is, however, different from true *Alsophila*, and is properly to be included in the genus *Metaxya* (p. 234). *Al. acaulis* and *Al.*

formosana have creeping rhizomes, but they show the characteristic anatomical structure of the Cyatheeae, and can be included in the true *Alsophila*. This point must be taken as distinguishing these two species from the ordinary ones with erect stems, and these species and others with creeping rhizomes, if any exist, may be included in a special section of the genus. A definite conclusion, however, cannot be reached until further observations on the genus have been made.

The genus *Cibotium* includes some species with dendroid trunks, while *Cib. Barometz* has a creeping rhizome. In this respect, this species may be distinguished from others with erect stems, and may be classified into a special section of the genus, as in the case of *Alsophila*. Moreover, this species differs anatomically from others in that, it has no sclerenchymatous sheath surrounding the stele (p. 277).

D. External Features of the Stem

The stem tapers toward the base, and thickens upwards gradually, so that the basal part of the stem is of a paraboloid form. But, on reaching a certain thickness, the stem retains this constant thickness up to the summit (Fig. 71). Such is the case with a stem of regular growth, but it is rather rare that such a form is actually found. As a matter of fact, the thickness of the stem is somewhat irregular throughout, showing constrictions in some regions. As the tree-fern makes no secondary growth, the parts once formed undergo no further changes, so that portions grown under unfavorable conditions remain permanently constricted.

The height of the stem in each species differs considerably. Generally speaking, the stems of the three species with creeping rhizomes are small, scarcely reaching 10 cm. in length, those of *Al. Ogurae* and *Al. podophylla* reach up to 2–3 m., and those of *Al. Bongardiana* and *Al. latebrosa* reach more than 10 m. in height.

The diameter of the stem in each species differs considerably. The maximum diameters observed are shown below :

Species	Diameter (mm.)	Species	Diameter (mm.)
Al. acaulis	20	*Al. formosana*	35
Cib. Barometz	50	*Al. Ogurae*	60
Al. podophylla	95	*Cya. spinulosa* (Bonins)	100
Cya. spinulosa (Ôsumi)	110	*Cya. spinulosa* (Formosa)	130
Al. Bongardiana	140	*Al. latebrosa*	155

The stem is sometimes covered with remains of petiolar bases, so that its surface is nowhere exposed, while in some cases leaves fall clear

from their very bases exposing the stem surface. In any case, in the basal part of the stem adventitious roots are borne on the stem, and cover it very thickly.

E. Relation Between the Stem and Leaves

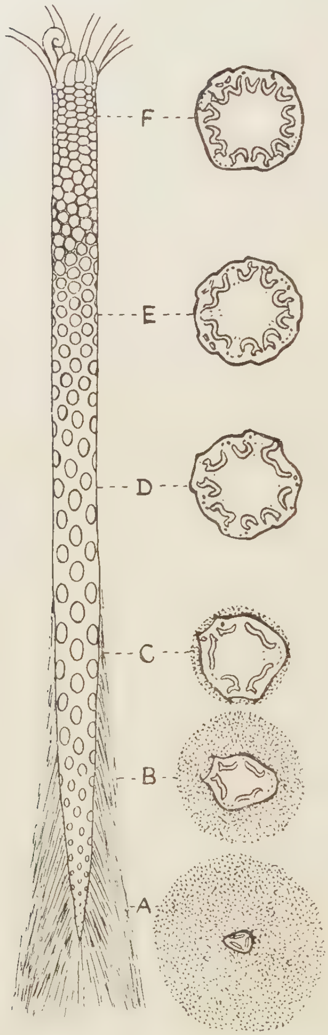

Fig. 71. A diagram of the Cyatheacean stem, showing the form and arrangement of leaf-scars, the position of roots and the outline of cross sections in different parts; cross sections A–F are taken at the levels of the stem shown A–F.
(Stem $\times \frac{1}{20}$; cross sections $\times \frac{1}{10}$).

Leaves are borne all around the stem radially, and even in the creeping rhizomes this relation holds good. After the leaves perish, the petioles may remain on the stem surface or fall off entirely. In the latter case, scars of the petiole are left on the stem surface, as in *Al. Bongardiana* and *Al. latebrosa.*

Phyllotaxy. The determination of the phyllotaxy is difficult when the petiolar bases are left on the stem, as they overlap one another. It is, however, easy when the scars on the stem surface are exposed. The phyllotaxy of the Cyatheaceae is of a relatively simple radial type, but varies according to different parts of the stem. As a matter of fact, it is not constant throughout the stem, but changes gradually from the stem base upwards. The change of the phyllotaxy occurs regularly in all of the species observed. In the basal or younger part, the phyllotaxy is $\frac{2}{5}$, but such a type is limited to a very short distance at the base, and the phyllotaxy changes gradually

upwards. The factor which causes the change consists in the decrease of the divergent angle. In the $\frac{2}{5}$ region, the sixth leaf from any leaf is situated exactly above the latter, while in somewhat higher region, the sixth leaf does not reach the perpendicular of the first, but is situated a little beyond it. The decrease of the angle takes place gradually, until a $\frac{3}{8}$ type is obtained. Of course, in the region intermediate between $\frac{2}{5}$ and $\frac{3}{8}$, transitional types are found. The region where the phyllotaxy becomes $\frac{3}{8}$ is not constant owing to the rate of growth. It is usually the part 0.5–1 m. above the base, so that in a small young specimen, and in three species with creeping rhizomes, the part with a $\frac{3}{8}$ phyllotaxy is not formed, and the upper part of the stem in such plants shows a type intermediate between $\frac{2}{5}$ and $\frac{3}{8}$. In taller plants, there is a region with a $\frac{3}{8}$ phyllotaxy, but it is limited to a short distance, and the phyllotaxy changes again upwards by the gradual decrease of the divergent angle. In such a way, in the upper part of a stem, 2–3 m. in height, the phyllotaxy becomes a $\frac{5}{8}$ type or a somewhat advanced form (Fig. 71, C). The stems of *Al. podophylla* and *Al. Ogurae* are of this type.

In the portion of the stem above this, the phyllotaxy becomes more and more complex, and at the same time irregularities may take place. In a higher portion, the leaves are arranged in ten regular vertical rows (Fig. 71, E). Further higher up, the phyllotaxy changes further, and leaves are arranged in eleven regular rows, and still higher it chages to the form, where the leaves are arranged in twelve or thirteen rows (Fig. 71, F). Such an arrangement in ten to thirteen rows may be derived from a $\frac{5}{8}$ type by an irregular displacement of the leaves as shown in the case of *Alsophila Bongardiana* (p. 239, Fig. 37). This type is found in *Cya. spinulosa, Al. Bongardiana* and *Al. latebrosa.*

So far as the writer has observed, thirteen vertical rows are the most advanced type of arrangement. Scott (1874) observed the phyllotaxy of the Cyatheaceae, and found a $\frac{1}{3}$ form at the basal part of the stem. The writer has never seen a case with $\frac{1}{3}$, instead it has always been $\frac{2}{5}$ that he has found in the basal part. Theoretically, the presence of such a $\frac{1}{3}$ type is impossible, for the divergent angle of the $\frac{1}{3}$ type is less than that of the $\frac{2}{5}$ type.

The direction of the phyllotaxy may be either left-handed or right-handed. Even in one and the same species, types with different directions are met with.

Size of the Leaf. The leaves which are found on the basal part of the stem are small; they become larger upwards in keeping with the enlargement of the stem. But it must be remembered that in the basal

part of the stem, with a $\frac{2}{5}$ phyllotaxy, a petiolar base can extend up to $\frac{1}{5}$ of the whole circumference of the stem, while in the part with $\frac{3}{8}$, it is only $\frac{1}{8}$ of the stem circumference that a leaf can occupy. In other words, the relative size of a leaf in the $\frac{2}{5}$ region is larger than that in the $\frac{3}{8}$ part ; consequently, in a cross section of the basal part of the stem, leaf-bases have a great influence on the outline of the stem, even producing an irregular triangular form (Figs. 71 & 72, A). Higher in the stem, the influence of the leaves on the stem becomes less, and the outline of the stem in a cross section becomes circular though some irregularities are found in the position of leaf-attachment (Figs. 71 & 72). In smaller young plants and in those with creeping rhizomes, as the phyllotaxy does not reach $\frac{3}{8}$, the cross section of the stem is triangular or pentagonal in all cases.

F. The Stele of the Stem

Cross Section. First, let us consider the form of the stele in cross sections. The stele lies near the periphery of the stem and follows the outline of the surface. In a stem with a triangular outline, the stelar ring is also triangular, and in one with a circular outline, the stelar ring is also circular (Figs. 71 & 72). The margins of the meristeles which face the leaf-gap curve outwards. The outward curving is not pronounced in the basal part, there, however, the influence of the leaf is so strong that the outline of the stele becomes triangular like that of the stem (Fig. 72, A). On the other hand, in a cross section of the stem in the higher part, though the influence of the leaf on the stem is not so prominent, the curving of the margins is rather marked ; moreover, as the leaves are closely arranged, leaf-gaps overlap one another, and the stelar ring is separated into small meristeles each having a semicircular or horseshoe-shape (Fig. 72, E–F).

The Leaf-Gap. Next, the solid construction of the stele will be considered. The stele is a hollow cylinder, the wall of which is perforated by numerous leaf-gaps. The stelar margin of the latter turns outwards. The form of each leaf-gap is fusiform, its size increasing almost in keeping with that of the stem. The arrangement of the gaps corresponds to that of the leaves. In the creeping rhizomes, in which the leaves are attached somewhat twisted, the real phyllotaxy can be determined only by the position of the gaps. The length of each gap is longer than that of the leaf-scar or the part attached by a petiolar base. A gap belonging to a leaf opens far beneath the petiolar base.

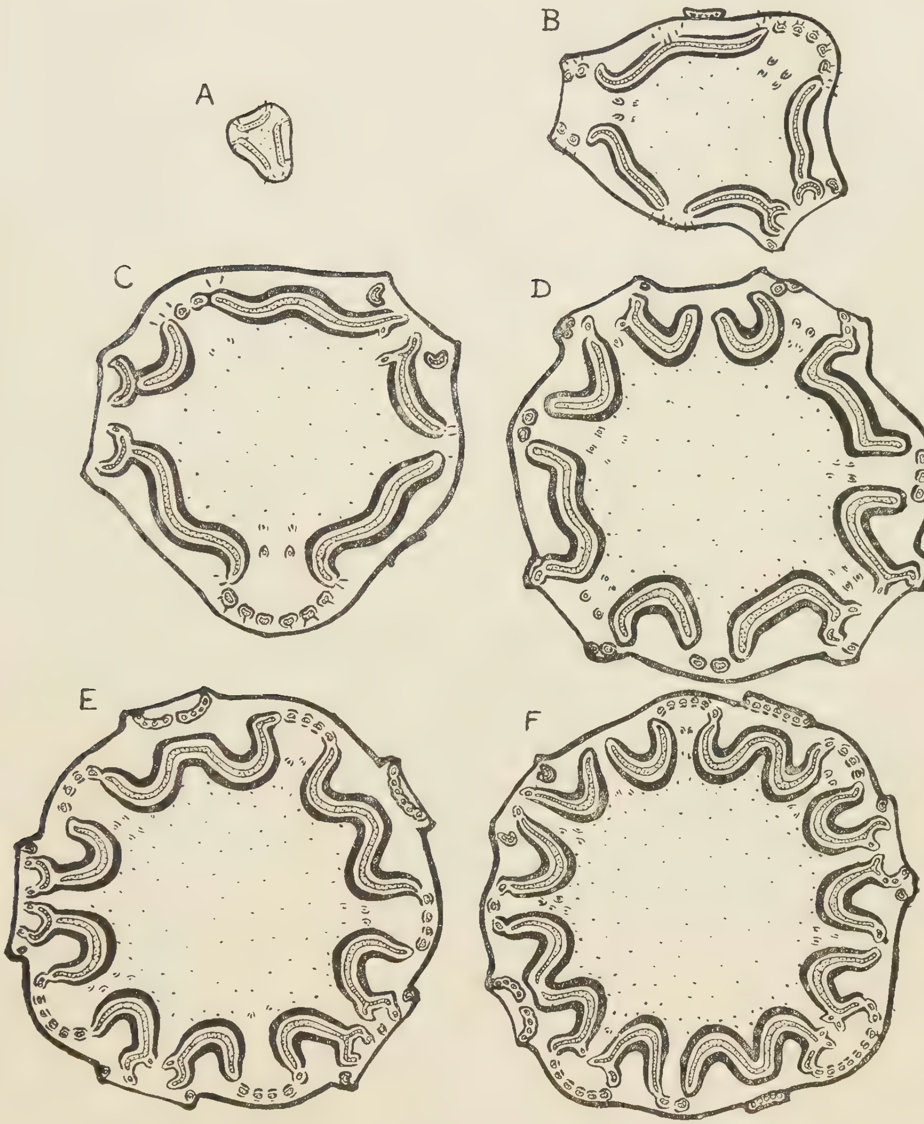

Fig. 72. Cross sections of different parts of the stem, showing the change of size and form, and the number and arrangement of leaf-gaps. These sections (A–F) correspond to the positions of the stem (A–F) shown in Fig. 71. They are drawn diagrammatically based on *Cyathea spinulosa*. $(\times\frac{1}{2})$

A, Base, covered with thick root-mass (omitted here); phyllotaxy $\frac{2}{5}$
B, About 0.7 m. above the base, covered with root-mass; phyllotaxy $\frac{2}{5}$–$\frac{3}{8}$
C, About 1.2 m. above the base, covered with roots; phyllotaxy $\frac{3}{8}$
D, About 1.8 m. above the base; phyllotaxy $\frac{3}{8}$–10 rows
E, About 2.3 m. above the base; phyllotaxy 10 rows
F, About 2.9 m. above the base; phyllotaxy 13 rows

Relation of Size of the Stem and the Stele. The relation of size of the stem and the stele in each species will be shown in the following table:

Species	Diameter of the stem (mm.)	Diameter of the stele (mm.)	Ratio
Cib. Barometz	30	20	1.50
" "	50	35	1.43
Al. acaulis	18	13	1.50
Al. formosana (Formosa)	35	22	1.59
" " (Ôshima)	40	28	1.43
Al. Ogurae	60	40	1.50
Al. podophylla	60	42	1.43
" "	93	72	1.29
Al. Bongardiana	70	55	1.27
" "	118	90	1.31
" "	140	115	1.24
Al. latebrosa	90	68	1.32
" "	120	80	1.50
" "	155	133	1.16
Cya. spinulosa (Hachijô)	62	43	1.45
" " (Bonins)	100	65	1.54
" " (Ôsumi)	110	70	1.56
" " (Loochoos)	65	45	1.44
" " (Formosa)	62	35	1.77
" " "	130	68	1.91

It will be seen from this table that, the ratio of the diameter of the stem to that of the stelar ring is usually 1.2–1.5, while the Formosa-type of *Cyathea spinulosa* shows a higher ratio, such as 1.8–1.9. It is also seen that, the ratio is smaller in the basal part than in the higher part of the stem. Such a relation is more accurately presented in the following table, in which the relation in four parts of one and the same plant of *Al. Bongardiana* is given (V, p. 237):

Region	I	II	III	IV
Distance from the ground (m.)	1.5	2.5	4.0	5.0
Phyllotaxy	$\frac{2}{5}$–$\frac{3}{8}$	$\frac{3}{8}$	10 rows	11 rows
Diameter of the stem (mm.)	138	120	120	110
Diameter of the stele (mm.)	115	95	85	80
Ratio	1.20	1.27	1.41	1.40

This change of the ratio may be caused by the fact that the meristele of the higher part curves semicircularly, its central part entering deeply into the pith (Fig. 72).

Ontogeny. The ontogeny of the stele is now to be considered. Fortunately, in most of the young plants, the pointed basal part remains undamaged, and the ontogeny of the stele as well as of the other tissues can be traced by means of cross sections at various parts of the stem. The very tip of the stem base, however, is so delicate that it has usually decayed. Generally, it is the part of the stem with a diameter of about 2 mm., where the internal structure can be most clearly recognized. In such a part, the stele, about 1 mm. in diameter, is constructed after the solenostelic type, the leaf-gaps being arranged in the $\frac{2}{5}$ manner. The state of the stele at the very base cannot be ascertained in ordinary material, but judging from the incomplete specimens observed by the writer, and from the observations of other authors it may be considered that the protostele at the very base becomes a solenostele by the appearance of the central parenchyma, and then of the internal phloem and endodermis. The writer has obtained the same result in adventitious buds found in *Al. formosana* and *Al. podophylla*. The solenostele thus formed enlarges in diameter, and by the overlapping of leaf-gaps, it changes into a dictyostele. The stele then thickens, and at the same time, the form of the leaf-gaps undergoes a gradual change by the characteristic outward curving of the stelar margin (Fig. 72).

G. The Sclerenchymatous Sheath of the Stem Stele

The presence of the brown sclerenchymatous sheath surrounding the meristele of the stem is one of the characteristics of the Cyatheaceae, but it is wanting in *Cibotium Barometz*. Without doubt, this tissue and the same tissue at the surface of the stem serve as a mechanical support of the large erect stem. One might ascribe the absence of this tissue in *Cibotium Barometz* to the creeping habit of the stem. But, such an explanation can hardly be accepted, because in two species of *Alsophila* with creeping rhizomes, this tissue is developed prominently. It is perhaps due to the peculiar nature of *Cib. Barometz* that this tissue is absent. In this connection, it may be suggested that this species may be classified as distinct form from other species of *Cibotium*, which have erect stems and are provided with sclerenchymatous sheaths. The absence of the sheath in the Cyatheaceae was formerly found in *Thyrsopteris elegans*, *Alsophila blechnoides* and *Cibotium Barometz*. The first is a monotypic species and the only representative of the tribe Thyrsopterideae, while the second is a species to be included in another genus, *Metaxya*. The separation of *Cibotium Barometz* from other

species of the genus, therefore, may be considered as a reasonable proposition (VII, p. 277).

The sclerenchymatous sheath surrounding the meristele is a special character of this family, for such a sheath is not found in other families of ferns, even in the species with erect stems.

Perforation. The sclerenchymatous sheath surrounds each meristele, from which it is separated by a layer of parenchyma. The sheath is, therefore, double-walled cylinder. Numerous small pores of the sheath which connect the inner cavity of the sheath and the cortex or the pith are found in the marginal parts at the leaf-gaps. These are the perforations through which leaf-traces, root-traces and medullary or cortical bundles penetrate, and all of them are small. On the main part of the sheath, no such perforations are usually found, but in a few species, e. g. *Al. latebrosa, Cya. spinulosa*, in the wall of the sheath on the pith-side, small perforations are found, always containing medullary bundles.

Denticulation. The inner surface of the sheath, that is, the side facing the meristele, shows a smooth outline in all caces, but the outer surface, that is, the side facing to the pith or the cortex, may show either a smooth outline or an irregular denticulation. The latter form is caused by the approach of the medullary or cortical bundles. When the medullary or cortical bundle approaches the sheath, it enters the latter forming there a small groove, and when the sclerenchymatous sheath surrounding the bundle is united to the sheath of the stele, the former produces a denticular formation on the surface of the latter sheath. The presence or absence of the denticular formation on the sclerenchymatous sheath is constant in each species, and this may be used, to some extent, for specific determination. The species which show such denticulations are *Cya. spinulosa* (Bonin-, Loochoo- and Formosa-types), *Al. Bongardiana* and *Al. latebrosa*.

The denticular formation of the sheath is much more prominent in the part with numerous medullary or cortical bundles; consequently, it is more marked in the older or higher part than in the younger or lower part. In an extreme case, when the groove of the sheath becomes very deep, the sheath is perforated entirely by the bundle, as in *Cya. spinulosa*, or temporarily the bundle is enclosed entirely in the sheath, as in *Al. Bongardiana* and *Al. latebrosa*.

Ontogeny. The ontogeny of the sclerenchymatous sheath can be traced by the observations of the young plants. In a part with a stelar ring of about 1 mm. diameter, no sclerenchymatous elements are found

in the fundamental tissue. In a somewhat higher part of the stem, sclerenchymatous masses make their appearance on both sides of the stelar ring in irregular distribution. These masses on each side of the stele gradually connect with one another to form a continuous band. This ontogenetical development of the sheath differs somewhat from that observed by some authors (e. g. STEPHENSON, 1908), who have described this tissue as appearing in the pith as a mass, in which parenchymatous elements appeared, so as to form a ring lining the inner side of the stelar ring. Such a mode of formation of the sclerenchymatous ring has not been observed by the writer in the young plant, but he has found it in adventitious buds of *Al. formosana*. Perhaps, both processes of the formation of the sclerenchymatous ring are possible.

H. THE LEAF-GAP AND THE LEAF-TRACE

Petiolar bundles of the Cyatheaceae are arranged, not in a simple form, but in one peculiarly complicated. Consequently, when leaf-traces are parted from the stelar margin, they exert an influence on the form of the leaf-gap. Moreover, the leaf-gap becomes complex by the fusion of medullary bundles.

The form of a leaf-gap and the mode of parting of leaf-traces differ considerably in different parts of the stem, being simple in the basal part. In the species which grow to a moderate size, such as *Al. Ogurae* and *Al. podophylla*, the most advanced type of the form of the leaf-gap and the mode of parting of leaf-traces are similar to those found in the lower or younger part of the more advanced species, such as *Cya. spinulosa*, *Al. Bongardiana* and *Al. latebrosa*. In the species with short stems, such as *Al. formosana* and *Al. acaulis*, the adult form of the leaf-gap is similar to that found in the younger part of other species. The adult form differs in each species of the Cyatheaceae observed by the writer, but they are constructed according to a definite type, so that, if a simple form, such as that found in *Al. acaulis*, is advanced, a more abvanced type, such as is found in other species, will be obtained.

The form of the leaf-gap and the mode of parting of leaf-traces in *Cibotium Barometz* differ from those of the Cyatheeae. Therefore, those of the latter will be first considered.

FORM OF THE LEAF-GAP. The form of the leaf-gap is fusiform in all cases, but its size differs considerably according to its age and size, and also to the arrangement of the leaves. Generally speaking, the stem about 0.5–1.0 m. above the ground has the largest gaps. This region

corresponds to that where the diameter of the stem is the greatest. From there downwards, the size of the gap decreases gradually to the smallest basal part, in keeping with the decrease of the stem size. From there upwards, on the contrary, though the stem size does not undergo a great change, the vertical length of the gap decreases due to the crowding of leaves or gaps. The leaf-scars of *Al. Bongardiana* and *Al. latebrosa* manifest this relation most clearly (p. 228, Figs. 35–37).

The leaf-gap is a fusiform perforation of the stelar wall, and the stelar margins on the lateral sides of the gap are prolonged outwards, and turn laterally in labial form. The outward turning occurs on the lateral sides of the gap, but is not a simple one, and at one part near the top, the turning recovers once. In this part, the two stelar margins approach each other in the median line of the gap, making the entrance of the gap narrower. The marginal bending on each side, therefore, is divided in two labial parts, the lower being always the larger and more prominent. Therefore, though the leaf-gap itself is fusiform, the stelar margin takes a gourd-shape (Fig. 73). The recovering part of the marginal turning is produced by the fusion of the medullary bundle.

Parting of the Leaf-Trace. Leaf-traces are parted from the stelar margin of the gap, and the traces parted from the upper and lower parts of the lateral constriction correspond to the superior and inferior strands. As the outline of the stelar margin is gourd-shaped, the parted traces are arranged in the same manner, each of the superior and inferior series being in an arc-shape.

The union with the medullary bundle exerts a great influence on the outline of the stelar margin. The medullary bundles fuse with the stelar margin at the upper half of the leaf-gap, and produce the leaf-traces belonging to the superior series. Schütze (1906) described a case in which the medullary bundle fuses with the stelar margin below the constriction of the marginal bending, but the writer has never seen such a case. It is the first pair of the medullary bundles that produces the lateral constriction of the marginal turning. The succeeding medullary bundles fuse with the stelar margin exerting no conspicuous influence on the stelar outline of the gap, and the fused parts are parted as leaf-traces. The last pair of the medullary bundles takes the same course as the first, and narrows the stelar gap. Some branches of the medullary bundles enter the petiole, without joining with the stele. These bundles, at most three or four pairs in number, are arranged in the petiole isolated in the upper part. The medullary

bundles which produce such particular traces are not special ones, but are branches of other bundles; when the branching takes place at a lower level, the exact relation is difficult to trace.

ONTOGENY. The ontogeny of the leaf-gap and the leaf-traces will now be considered. Generally speaking, in the younger basal part of the stem, the leaves are small in size, the leaf-traces less numerous, and the mode of parting of the traces is simple. *Al. Bongardiana* and *Al. latebrosa* are of the most advanced type, and the type of *Al. Ogurae* and *Al. podophylla*, with a stem of moderate size, is simpler than the former two, but the type of these species is the same as that found in the lower younger part of the former two. *Al. acaulis* and *Al. formosana*, with small stems, have a very simple type, but such a type may be found in the lower younger part of other species. Therefore, the ontogeny of the leaf-gap and the leaf-trace of anyone species can be applied to all the species of the Cyatheeae.

In the smallest leaves, only one pair of petiolar bundles is found. The leaf-gap corresponding to it is small and fusiform, and from its lateral margins leaf-traces are parted. In the case with two pairs of petiolar bundles the lateral margins of the gap protrude, and give off two pairs of traces, which are arranged in a circular form in the petiole (Fig. 73, A). In the case with three or four pairs of petiolar strands, the same process of parting of traces is repeated (Fig. 73, B). The size of the gap becomes larger, and the number of traces parted from it becomes more numerous. Meanwhile, the form of the gap is influenced by the formation of medullary bundles. The medullary bundle makes its appearance usually at the region where two or three pairs of leaf-traces are parted from the gap (Fig. 73, C). When only one pair of the medullary bundles is present, it fuses to the stelar margin at the upper corner of the gap, the fused part being parted as the last leaf-trace situated in the petiole at the upper median part (Fig. 73, C). This type is found in the adult form of *Al. acaulis* and in the young form of other species of the Cyatheeae. In a somewhat advanced form, the medullary bundle bifurcates, and one branch fuses with the upper part of the gap, while the other branch fuses with the lateral side of the gap. By the fusion of the latter the lateral turning of the stelar margin recovers, corresponding to the constriction of the marginal turning, and the petiolar bundle which is derived from this part projects somewhat inwardly (Fig. 73, D). This is found in adult form of *Al. formosana*. The lateral constriction of the stelar turning or the internal projection of the lateral petiolar bundles, however, is not

always derived from fusion with a medullary bundle, and even in a gap without such a bundle the corresponding projection or constriction may be found, as in *Al. acaulis* and *Al. Ogurae.*

In a more advanced form, the gap becomes larger, and the outward curving of the marginal part becomes prominent; consequently, the lateral constriction due to the fusion of the medullary bundle becomes more and more pronounced. At the same time, the traces in each gap become numerous, and the inferior strands are arranged in an arc, while the superior ones show a lateral projection consisting of one or two pairs of strands (Fig. 73, D–E).

In a more advanced form, in keeping with the increase of the size of the gap, the outward turning of the lateral margin as well as the lateral constriction of the marginal turning becomes prominent, so that from the upper region of the constricted part, two or three traces are parted, which are situated in the petiole projecting inwards, and at the same time the last pair derived from the fusion of the last medullary bundle is also directed inwardly (Fig. 73, E).

Then, by the acceleration of the marginal turning, the lateral constriction becomes more marked, and the traces derived from the constricted region are not only the two or three on its upper side, but one trace on its lower side shows the internal projection, the latter corresponding to the last inferior strand (Fig. 73, F). Thus, the inferior projection of the petiolar strands on the lateral sides may be said to follow the superior one. Meanwhile, the medullary bundles increase in number, those belonging to a gap amounting to three or four pairs, the first of which gives off the first superior trace, and the last the last, the intermediate one producing the intermediate trace of the superior series (Fig. 73, F). Sooner or later, however, the branching of the last medullary bundle takes place at a short distance from its end, and the branch thus formed enters the petiole directly as an inwardly projecting leaf-trace at the median upper part (Fig. 73, E–F). The main bundle takes the ordinary course, and gives off the trace at the median upper part. The branching of the bundle takes place near its end, so that the petiolar strands derived from the main bundle and its branch approach each other. In this case, the superior strands are arranged in the Γ7-shape, of which the short arm is derived from the upper projection just referred to, and the longer arm from the lateral projection (Fig. 73, E). This type of leaf-gap is found in the adult form of *Al. Ogurae* and *Al. podophylla.*

In a more advanced case, the branching of the last medullary bundle takes place far below its end, so that two pairs of petiolar

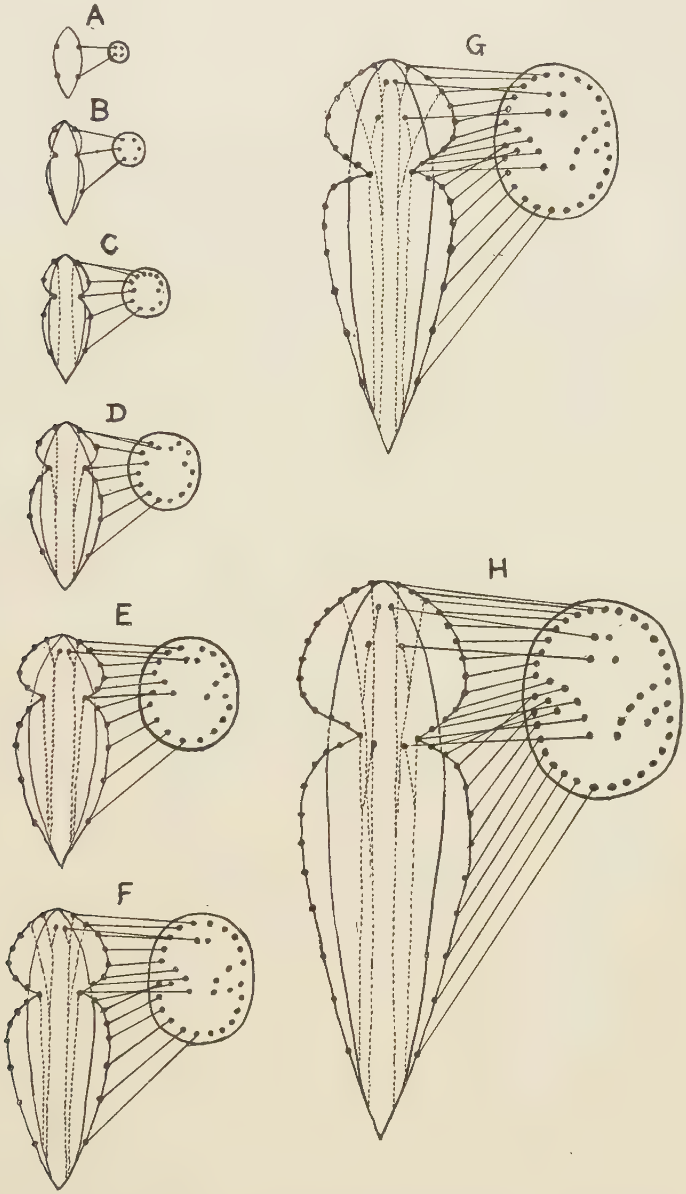

Fig. 73. A diagrammatic representation of the ontogeny of the construction of leaf-gaps, the parting of leaf-traces and the arrangement of petiolar strands. The base of a leaf-trace and the corresponding petiolar strand are connected by a straight line. Dotted lines denote the medullary bundles. $(\times \frac{2}{3})$

strands, derived from the main bundle and its branch, are separated from each other, the strand derived from the latter being deeply isolated inwards (Fig. 73, F). Meanwhile, the branching of the medullary bundle propagates to the preceding bundle of the last one, and its branch enters the petiole directly, and becomes an isolated strand situated a little below the former isolated one (Fig. 73, G). This type is found in *Cya. spinulosa.*

Al. Bongardiana and *Al. latebrosa* have the most advanced and complicated type. In keeping with the enlargement of the leaf-gap and the increase of the number of leaf-traces, the lateral projection of the leaf-gap becomes prominent. The laterally projecting strands in the petiole consist of more than ten pairs of strands ; consequently, the inferior row of the lateral projections increases to two or three pairs. The isolated upper strands, having no direct connection with the stele, amount to as many as four or five pairs (Fig. 73, H). This is the adult type found in these two species, and is also the most advanced type found in Japanese Cyatheeae. Of course, in the young stages of these species, the simpler form, such as has been previously described, is found.

In short, the form of the gap and the mode of parting of leaf-traces in the adult plants differ in different species, but they all show the same type in the ontogeny. In the youngest part, all species show the simplest construction. In *Al. acaulis* and *Al. formosana*, which do not grow large, the development of the leaf-gap is not advanced, while in other species, the constriction of the gap becomes complex, until such a type as is found in *Al. Bongardiana* and *Al. latebrosa* is obtained.

CIBOTIUM. Let us now compare the leaf-gap of *Cibotium Barometz* with that of the Cyatheeae. The most important difference between them is that, (a) the outward curving of the stelar margin takes place on the lateral sides of the gap in the Cyatheeae, but on all sides in *Cibotium*, so that in the latter, the boundary between the gap and the stele is not distinct, and that (b) in *Cibotium*, the lateral projection of the stelar margin is not pronounced owing to the absence of the medullary bundle. In the case of *Cibotium*, on the lower side of a gap, the stelar ring bulges out, producing no distinct boundary between the stele and the trace, while at the upper part of the gap, a constricted region may be found between the stele and the bulging part. A little higher up, the inside of this constricted part projects internally in a hook-form, and the leaf-trace is then separated from the stele, leaving a leaf-gap. The separated trace is then divided into numerous strands arranged in a heart-shape. In this case, a few traces on the lateral

sides project slightly inwards, corresponding to the characteristic projection in the Cyatheeae.

If the division of the leaf-trace takes place at the lowest part of the gap, a leaf-gap similar to that of the Cyatheeae will be established. In *Cibotium*, the lateral projection is present, though it is not prominent, while the upper projection is very prominent. In the Cyatheeae, both the lateral and upper projections are very prominent, and they seem to be derived from the fusion of the medullary bundles. But in *Cibotium*, the medullary bundle is absent, so that the inward projection is developed without any relation to the medullary bundle.

The ontogeny of the leaf-gap and the mode of parting of leaf-traces in *Cibotium Barometz* is far simpler than those of the Cyatheeae, owing to the absence of the medullary bundle. In the smallest gap, the lateral sides of the stelar margin project as a pair of leaf-traces. Proceeding upwards, in keeping with the increase of the size of the gap, the marginal turning takes place, and two or three pairs of leaf-traces are arranged in a circular form. In a somewhat more advanced type, the upper projection appears first, and then the lateral one, and thus the adult form is produced gradually.

Limit of the Leaf-Gap. From a comparison of the leaf-gap and leaf-traces of the Cyatheeae and *Cibotium Barometz*, the following results have been obtained. The distinction of the leaf-gap and leaf-traces is easily made in most of the ferns, but it is not so easy in the Cyatheaceae. It is uncertain whether the part of the stelar margin that turns laterally at the gap in the Cyatheeae is a part of the stele or of the leaf-traces. It may be thought that, on the one hand, this part is the margin of the stele, and the strands parted from its margin are traces, or on the other hand, it may be regarded as the basal part of a connected leaf-trace, the stelar part being limited to the entrance of the gap, which is fusiform. The writer once held the former view, and gave a description in that sense, but from a comparative study with *Cibotium Barometz*, he is now inclined to the latter view. In the parting of leaf-traces of *Cibotium*, the stelar part bordering the gap bulges out in the form of a band. If this part enters the petiole undivided, it will produce a simple leaf-trace, as found in some Polypodiaceae. The division of the trace, therefore, is not the absolute condition of the leaf-trace. In the Cyatheeae, as the basal leaf-traces of a leaf-gap are parted from its very margin, the writer has extended this conception to the parting of the lateral traces, the undivided part being considered as the stelar portion; while in *Cibotium*, the separated

strands are not detached from the gap itself, so that the projecting part may be considered a part of the leaf-traces as yet undivided.

The upper and lateral projections of the stelar margin of the leaf-gap will now be considered. It seems that, in the Cyatheeae these projections may be produced by the union of the first and last medullary bundles, while in *Cibotium* both projections are present, notwithstanding the absence of the medullary bundle. Thus, these projections of the leaf-gap margin and the leaf-traces may be the peculiar nature of *Cibotium*, and may be exaggerated by the union of the medullary bundle in the Cyatheeae. In the latter tribe, it is the first and the last bundles which contribute to the formation of the projections, the other bundles having no influence on the form of the stelar margin of the gap.

I. The Medullary Bundle

The presence of medullary bundles in the stem is one of the characteristics of the Cyatheeae. Their number differs considerably according to the size and age of the stem. Generally, the medullary bundles are more numerous in the larger or older parts than in the smaller or younger parts. In the pith, they are connected with one another in a complex network. In some cases, each of the medullary bundles is protected by a brown sclerenchymatous sheath. The latter surrounds the bundle in a ring-form, or shows a small arc-form, but some bundles are not provided with it. The presence or absence, the form and distribution of the sheath is so constant in each species, that these characters may be used for specific determination.

Number. The relation between the size of the stem or the stele and the number of medullary bundles in a cross section of the stem is shown in the following table:

Species	Diameter of the stem (mm.)	Diameter of the stele (mm.)	Number of medullary bundles
Al. acaulis	18	11	6
" "	20	12	10
Al. formosana	35	22	30
" "	40	28	80
Al. Ogurae	60	40	70
Al. podophylla	60	42	150
" "	93	72	190
Al. Bongardiana	70	55	100
" "	118	90	185
" "	140	115	228
Al. latebrosa	90	68	116
" "	120	80	322
" "	155	133	370
Cya. spinulosa	100	65	130
" "	75	53	117

From this table it is evident that, though the bundles are numerous in the larger stems, there is no specific difference in their number. The medullary bundles are distributed uniformly in the pith. In the smaller stems, they are found in the central part, while in the larger ones, they are arranged also in the periphery of the pith, being in contact with the inner surface of the sclerenchymatous sheath of the stele. In extreme cases, they dip into the sheath, forming there small grooves, and moreover, when the bundles are accompanied by the sheaths, the latter connect with the same tissue of the stele, making the irregular denticulation on the sheath of the stele.

Course. The tracing of the whole course of medullary bundles is very difficult, as they are numerous and small, connecting with one another in a network. The medullary bundle appears in the pith, and ascends through it up to a leaf-gap, in whict it fuses with the stelar margin. The number of the bundles which belong to each gap varies from one to ten pairs, but they do not always represent independent bundles, as some are branches of the others. The branching and fusion of the bundles to form a network take place very irregularly. In any case, the upper ends of the medullary bundle fuse with the stelar margin of the upper half of the leaf-gap, and the fused part gives rise to a leaf-trace belonging to the superior series. Of the medullary bundles belonging to a gap, the first fuses with the laterally constricted part of the marginal stelar turning, and makes the constriction prominent, and the very tip of the constricted part thus formed parts as an inwardly projecting leaf-trace, i. e. the first superior strand. This leaf-trace, therefore, may be thought to be derived from the first medullary bundle. The last medullary bundle of a leaf-gap fuses with the stelar margin at the upper part of the gap, and the fused part is parted as a leaf-trace situated at the upper median corner. The intermediate bundles belonging to a leaf-gap fuse with the stelar margin at some parts of the superior region, and produce some intermediate leaf-traces of the superior series. The last two or three medullary bundles, however, bifurcate before they end, and their branches enter the petiole directly, without connecting with the stelar part, and become the isolated leaf-traces situated under the upper sheet.

Ontogeny. The mode of development of the complicated course of the medullary bundle can be understood by the ontogenetical study of an individual plant (Fig. 73). In the young part of the stem, in which one or two pairs of leaf-traces are found in each gap, no medullary bundles are found (Fig. 73, A–B). The part where the bundle

makes its appearance is not constant, as the following table shows :

Species	Distance from the basal tip (mm.)	Diameter of the stem (mm.)	Diameter of the stele (mm.)
Al. acaulis	30	10	5
Al. formosana (Formosa)	9	7	3
" " (Ôshima)	—	8	4
Al. Ogurae	—	8	4
Al. podophylla	20	12	5
Al. Bongardiana	—	6	3
Al. latebrosa	—	4	2
Cya. spinulosa (Hachijô)	6	8	4
" " (Formosa)	—	6	3

At first, the medullary bundles appear in the pith, usually in pairs, and ascending through the pith along the leaf-gap fuse with the upper stelar margin of the gap. Such a part is separated as a leaf-trace, situated at the upper median part, i. e. the last leaf-trace (Fig. 73, C). This state is found in the adult stem of *Al. acaulis*, and in the young part of other species. The length of the medullary bundle is nearly equal to that of the gap, but it elongates gradually upwards. In some parts, the medullary bundle bifurcates before ending, but two branches fuse again into one strand, which fuses with the stelar margin. This form is found in the young stem of *Al. Ogurae*. The case in which the bifurcated branches fuse again represents a step transitional to the next. In the next type, each of the bifurcated branches ends separately, and produces a leaf-trace, the former branch the first trace, the latter branch the last trace of the superior series. In this case, the superior strands of the petiole reach three to five pairs, and the first and last pairs, which are derived by the union of the medullary bundles, project inwards somewhat from the lateral and upper sides (Fig. 73, D). In some cases, the stage in which the bifurcated strands fuse into a single strand is omitted, and the bifurcated condition comes soon after the undivided case. In this stage, the leaf-gap elongates, and the medullary bundles attain a length nearly twice that of the corresponding gap, so that it becomes difficult to trace the whole course of the bundle. Moreover, an irregular division and interconnection of the bundles takes place, which makes the tracing more difficult. This condition is found in *Al. formosana*, in which usually two pairs are found in each gap, producing the first and last traces of the superior strands (Fig. 73, D).

Sooner or later, an interesting change appears. The last medullary bundle belonging to a gap gives off a strand, which enters the petiole directly, without connecting with the stele, and within the petiole it projects from the upper median part (Fig. 73, E). Such a branching

is found in *Al. Ogurae* and *Al. podophylla.* In the former, the branching makes its appearance in the case with one pair of medullary bundles, but in the latter, the upper of the two pairs of medullary bundles bifurcates before its fusion. In both cases, traces are derived from the bundles, and branches are arranged in the petiole on the upper side, from which they project like hooks. (Fig. 73, E). At the same time, the branching of the medullary bundle is repeated, and at a certain stage, there are bundles with three endings or branches, which fuse with the stelar margin respectively; the first branch producing the first superior trace, the last branch the last trace, and the intermediate one a certain trace of the superior series (Fig. 73, F).

In a more advanced case, branching such as is found in the last bundle takes place in the preceding bundle, and the trace derived from the branch is isolated at the upper median part of the petiole. In this case, the trace produced by the main strand of the last bundle is situated at the upper part and does not project inwards, and the traces derived from the branches are quite isolated (Fig. 73, G). This is the condition found in the adult plant of *Cya. spinulosa.*

In the next stage, the medullary bundles belonging to a gap amount to more than five pairs, some of which give off branches, which enter the petiole directly, and within the latter remain isolated from the other strands (Fig. 73, G–H). This condition is found in *Al. Bongardiana.* The same branching of the medullary bundle occurs near the end of the first medullary bundle, and the branch thus formed, without communicating with the stele, becomes the first superior leaf-trace, while the main bundle fuses with the stele as usual, and produces the second leaf-trace (Fig. 73, H). This form is found in *Al. latebrosa,* and is the most advanced type found in Japanese Cyatheeae.

In short, the course of the medullary bundles becomes more and more complex in keeping with the growth of the stem, until its regularity is disturbed by their repeated division and intercommunication. They arise in the pith independently, and ascending through it enter the petiole as leaf-traces, which are of two kinds according to their behavior at the gap; for one kind fuses with the stelar margin at the leaf-gap, while the other enters the petiole directly without touching to the stem stele. In all cases, the leaf-traces derived from the medullary bundles belong to the superior series. The traces of the latter kind are derived from the branching of those of the former kind, and are situated in the

petiole at the upper median part as inward projections or as isolated bodies, sometimes also they appear at the top of the laterally projecting series.

Irregularities. The course of the medullary bundles shows irregularities, of which some instances will now be given. (a) The repeated division and interconnecting of medullary bundles begin usually at a point remote from the stem tip, but sometimes these processes takes place early in the stem tip. This is found especially in *Al. Bongardiana* and *Al. latebrosa.* (b) In some cases, in the region where the bundle should be bifurcated, it trifurcates. (c) The most pronounced case of irregularities is that in which the upper end of the bundle ends blindly in the pith quite unconnected with the stele. This is found sometimes in *Al. acaulis.* (d) Though the lower end of the bundle appears in the pith independently, some bundles arise as internal thickenings of the stelar ring. This form is found, though rarely, in the young part of *Al. Ogurae.*

In some former observations (De Bary, 1877; Schütze, 1906), there is a different opinion as to the course of medullary bundles. Concerning their upper ends, the medullary bundles were thought to enter the petiole directly, to form isolated leaf-traces, or to connect temporarily in their course with the stelar margin at the leaf-gap, or with the stele itself with no direct connection with the gap. Though the two former cases have been observed by the writer, he has not met with an example of the last case. Concerning the lower ends, the bundles were thought to end blindly in the pith, or to be connected with the stele itself. But, the latter type has not been observed by the writer, except in the young part of some species.

Phylogeny. We are now in position to consider the phylogeny of the medullary bundles. Among the ferns, the plants which are provided with the medullary bundles are all members of the Marattiaceae and Matoniaceae, some of the Polypodiaceae and some others. In these cases, the medullary bundles are relatively few in number, and originate as internal thickenings of the stelar ring. The complicated stelar system thus formed is usually called the 'polycyclic stele'. The medullary bundles of the Cyatheeae differ from those of this polycycly; they are very small and numerous, and show the irregular arrangement, moreover, they arise in the pith independently, with no direct connection with the stele. In this point, the stelar system of the Cyatheeae differs from the normal polycyclic stelar type, and for it has been proposed by the writer the name "Cyathean Dictyostele" (II, p. 202).

Now, what relation is there between the polycyclic dictyostele and Cyathean dictyostele? As the origin of the medullary bundle cannot be considered to be of the same type, these two types are different from each other. The ontogenetical study of the stem-stele of *Al. Ogurae* gives a very interesting result. In the young part of this species, some of the medullary bundles do not arise in the pith independently, but appear as internal thickenings of the stelar ring. Such a mode of formation of the medullary bundle is limited to some leaf-gaps in the basal part of the stem, and for a little above the base the bundle appears independently in the pith. If the hypothesis that the young part of a plant shows a type derived from an ancestor of the plant may be accepted, it may be considered that, the Cyathean dictyostele is derived from the polycyclic dictyostele. Another, but similar, phenomenon has been found in certain species, though it is very rare; in the young part of the stem, at the level where the medullary bundle will appear, there has been observed a small protuberance on the inner surface of the stelar ring. This protuberance suggests a primitive feature and the first step in the bundle-formation, such as is found in *Al. Ogurae*, but in this case the protuberance disappears sooner or later without forming a separate medullary bundle.

J. The Cortical Bundle

Though the medullary bundle is found in all species of the Cyatheeae, the cortical bundle is limited to a few species of this tribe. Cortical bundles had been found by previous authors in a few species such as *Al. aculeata*[1], *Al. caracasana*[1], *Al. eriocarpa*[2], *Al. crinita*[3], *Cya. Imrayana*[3,4], *Cya. usambarensis*[3], etc., but a detailed explanation of their structure was not given.

Among the Japanese Cyatheeae, the writer has found cortical bundles in *Al. Bongardiana*, *Al. latebrosa* and *Cya. spinulosa* (Bonin-type). The course and other features of the cortical bundles in the two former species differ considerably from those of the last species, so that they must here be described separately.

In *Al. Bongardiana* and *Al. latebrosa*, they appear in contact with the outer surface of the outer sclerenchymatous sheath of the stele, and

1) Reichert (1859) Densk. math.-phys. Kais. Akad. Wiss., 17.
2) Lachmann (1889) Paris.
3) Schütze (1906) Beitr. wiss. Bot., 5.
4) De Bary (1877) Vergl. Anat.

ascend through it enclosed in sclerenchymatous sheaths. Then, they approach the leaf-gap, and finally fuse with the stelar margins of the gap. The connected parts of the stele are soon parted as leaf-traces situated at the lateral corners of the superior series. The behavior of the cortical bundle is rather simple, and does not differ much in stems of different ages and sizes. In *Al. Bongardiana*, one pair of cortical bundles is found in each gap, but in *Al. latebrosa* there are two pairs. In the latter species, two pairs of bundles are produced by the division of one pair of the cortical bundles, but the two branches are fused together near their upper ends, so that it is again only one pair that fuses with the stelar margin. Prior to the fusion with the stele, the cortical bundle connects with the stelar margin of the inferior region, but this fusion is always temporary.

In *Cya. spinulosa*, the occurrence of the cortical bundle is very inconstant. They are found in the Bonin-type collected from the Bonin Islands, and from other places (VI, p. 262). They appear in the cortex in contact with the sclerenchymatous sheath of the stele, and ascend through the cortex, dividing and uniting with one another, and finally fuse with the stelar margin, or with the bases of the leaf-traces. In each gap, there are two or three pairs of cortical bundles, but they fuse together at their upper ends into one or two pairs. The leaf-traces, which are joined with the cortical bundles, are situated at the lateral corners of the inferior series, and no cases are met with, where the bundles connect with the superior series.

The number of cortical bundles in various parts of three species may be stated as follows:

Species	Diameter of the stem (mm.)	Diameter of the stele (mm.)	Number of cortical bundles
Al. Bongardiana	70	55	9
" "	118	60	19
" "	120	83	50
Al. latebrosa	90	68	10
" "	120	80	72
" "	155	133	34
Cya. spinulosa (Bonins)	75	50	18
" " "	100	65	90
" " (Ôsumi)	85	60	0
" " "	110	70	24
" " (Ôshima)	75	43	1
" " (Loochoos)	65	45	1

The cortical bundles make their appearance far later or in a region higher up than the medullary bundles, as is shown in the following table; the region of the appearance of cortical bundles in *Cya. spinulosa* is very inconstant, and cannot be given here:

Species	Distance from the basal tip (mm.)	Diameter of the stem (mm.)	Diameter of the stele (mm.)
Al. Bongardiana	85	50	40
Al. latebrosa	—	35	23

The cortical bundles may or may not be enclosed in sclerenchymatous sheaths. The former case is found in *Al. Bongardiana* and *Al. latebrosa*, and the latter case in *Cya. spinulosa*. In the former two species, the sheath is very distinct, and shows a circular outline.

The cortical bundles found in the Cyatheeae are not found in any other groups of the ferns. Thus, for the stelar system consisting of the main dictyostele, accompanied by medullary as well as cortical bundles, the writer has proposed the name "Alsophilan Dictyostele" (V, p. 260).

K. External Features of the Leaf

The size of the leaves shows considerable variation due to the height or size of the stem. In the species with creeping rhizomes, the leaves are relatively small, and even in the other species, those borne on the younger part are also small. The largest leaves in each species have the following value, in which the approximate value of the whole length of the leaf-axis and the diameter of the petiolar base are given:

Species	Length of the leaf-axis (m.)	Diameter of the petiolar base (mm.)
Cib. Barometz	2.5	45
Al. acaulis	1.0	4
Al. formosana	2.0	11
Al. Ogurae	3.0	30
Al. podophylla	3.0	25
Al. Bongardiana	3.0	45
Al. latebrosa	3.0	65
Cya. spinulosa	3.0	45

The leaves are always compound with stout petioles, the basal parts of which are usually covered with scales. The ratio of the length of the petiole to that of the rachis in each leaf is not constant, but as a rule, the petiolar part of a leaf on a creeping rhizome, or on a short stem, is relatively long, occupying more than half the whole length of the leaf-axis, while the petiole of a leaf on a large erect stem is relatively short, occupying less than half the whole length, and, in extreme cases, only one-tenth of the whole length of the leaf-axis. In the former case, as the stem is small or creeping, a long petiole is necessary to keep the

lamina perfect, while in the latter a long petiole is not necessary as the stem grows high. The lamina is of a di- or tri-pinnate form.

The surface of the petiole is coloured. It is green in *Al. Bongardiana*, *Al. latebrosa* and *Cib. Barometz*, brown in *Cya. spinulosa*, and dark violet-brown in *Al. acaulis*, *Al. formosana*, *Al. Ogurae* and *Al. podophylla*.

The surface of the petiole is also characterized by protuberances, the size and shape of which may be used for specific determination. In *Al. acaulis*, *Al. formosana* and *Cib. Barometz*, the petiolar surface is devoid of protuberances, in *Al. Bongardiana* and *Al. latebrosa* the surface has numerous wen-like processes, in *Al. podophylla* and *Al. Ogurae* it is provided with numerous small spines, and in *Cya. spinulosa* the petiole is prominent owing to large hard spines.

When the young leaves are coiled up, they are closely covered with scales, most of which fall off at the time of their unfolding. In *Cib. Barometz*, no scales are found, and there are only golden filiform hairs on the petiole as well as on the stem.

L. The Vascular Strand of the Leaf

The number and arrangement of vascular strands in the petiole and rachis differ considerably according to the age and the size of the leaf, even in different parts of one and the same leaf.

Petiolar Base. First, let us consider the state of the vascular strands at the basal part of the petiole. The largest petioles of *Al. acaulis* and *Al. formosana*, the diameter of which is less than 10 mm., have less than ten pairs of vascular strands, showing the characteristic arrangement of the Cyatheaceae. Half of them are arranged at the lower side in an arc, while the upper half consists of strands arranged in a Γ7-form, that is, one or two pairs project inwards at the upper and lateral sides (Fig. 74, a C). On the other hand, the petiolar bases of *Al. Bongardiana* and *Al. latebrosa* contain more than fifty pairs of strands, most of which are arranged in a circle at the periphery, but some project from the lateral and upper sides. These strands projecting from the upper side, consisting of from two to four pairs, are isolated under the series of strands in the upper sheet. The laterally projecting series consists of two rows, the upper of which consists of ten or more pairs of strands, and the lower of from two to four (Fig. 74, a A). In other species having petioles of a size intermediate between the former two types, the number and arrangement of petiolar strands show the form intermediate between these types (Fig. 74, a B).

THOMAE (1886) differentiated the vascular strands of the petioles of the Cyatheaceae into superior and inferior strands, by means of the lateral projections. According to this nomenclature, in the petiole of *Al. Bongardiana*, the upper row of the lateral projections, the upper sheet and isolated upper strands constitute the superior strands, while the lower row of the lateral projections and the lower sheet mark the inferior strands. In the petiole of *Al. acaulis* and *Al. formosana*, the inferior strands consist of those arranged in an arc, while the superior ones are in the Γ7-form, the longer arm of which corresponds to the lateral projection, and the shorter one to the upper projection. The last form of arrangement is also found in the young petioles of other species.

ONTOGENY. The ontogeny of the petiolar strands can be traced by a comparison of petioles of different ages and sizes (Figs. 73 & 74). In the bases of the smallest petioles, there is only one pair of strands. In a somewhat larger petiole, there are from two to four pairs of strands, arranged in a simple circular form (Fig. 73, B–C). In the petiole with five or six pairs of strands, one pair at the lateral sides projects somewhat inwards, which is the sign of the lateral projection of the superior strands (Fig. 73, C).

In the next stage, the petiolar strands increase in number, the lateral two or three pairs project inwards, and one pair in the median upper part shows a tendency to incurving, the superior strands being arranged in the Γ7-form (Fig. 73, D–E). This type of arrangement of the strands is found in the adult petiole of *Al. acaulis* and *Al. formosana*. In the more advanced form, in keeping with the increase of the strands, the inward projections on the lateral and upper sides become prominent, to form the Γ7-shaped superior series, and in the inferior series, one pair at the lateral corner shows a tendency to incurving, arranged under the lateral projection of the superior series (Fig. 73, E). This form is met with in the adult form of *Al. podophylla* and *Al. Ogurae*. In this case, the lateral projection of the inferior series seems to be derived from the projection of the superior series. In the next stage, the increase of the strands makes the inward projections prominent, and one or two pairs of the upper projections are entirely isolated under the upper sheet (Fig. 73, F).

In *Al. Bongardiana* and *Al. latebrosa*, the whole number of strands amounts to as many as fifty or sixty pairs, sometimes even more than seventy pairs. The lateral projections are very prominent, the upper being more than ten pairs, and the lower about five pairs, while the upper isolated strands are from three to five pairs (Fig. 63, G–H). This

is the last or most advanced arrangement of petiolar strands in Japanese Cyatheeae.

Briefly speaking, the origin from which is derived this complex arrangement of strands lies in the formation of the lateral projections, and in that of the upper projection. These projections have a close relation to the appearance of the medullary bundles, but the lateral projection is not always derived from the fusion of such bundles, as is the case in the petiole of *Al. Ogurae* and in the young petiole of other species.

CIBOTIUM. The arrangement of vascular strands in the base of the petiole of *Cibotium Barometz* will now be considered. Though the stem of this species is small, the leaves are relatively large, and show a quite advanced type of vascular strands. In the base of a large petiole, numerous strands ranging from ten to twenty pairs are arranged almost in the same manner as in the Cyatheeae; two series of them are distinguished, viz. the inferior and the superior. The inferior series are situated on the lower side in a semicircular form, the marginal one projecting somewhat inwards, while the superior series show the lateral and upper projections, the former consisting of two or three pairs, and the latter of several pairs. The upper projection is very prominent, some pairs of strands projecting inwards deeply. They are not isolated, and connect with the series of strands of the upper sheet in a hook-shape. The general arrangement is, therefore, like that of *Al. Ogurae* or *Al. podophylla* (Fig. 74, a D).

The ontogeny of petiolar strands in *Cibotium* is also similar to that of the Cyatheeae, but the upper projection appears earlier than the lateral one. The projections in the Cyatheeae are believed to be derived from the fusion of medullary bundles, while in *Cibotium* these bundles are wanting, and the projections in this species have no relation to the medullary bundle.

UPPER PARTS OF THE LEAF-AXIS. The above statements relate to vascular strands in the basal part of the petiole. Proceeding upwards in the petiole, the number and arrangement of strands undergo a gradual change, which takes place in a similar manner in all species of the Cyatheeae, but differently in *Cib. Barometz* (Fig. 74). In the Cyatheeae, the number of strands diminishes gradually owing to the fusion of neighbouring strands. Then, the neighbouring strands join from end to end, to form a wavy connected band. This wavy connection of the strands takes places in the superior and inferior series respectively. In this case, the strands belonging to the inferior series become connected in their original position, so as to form a semicircular band with incurved

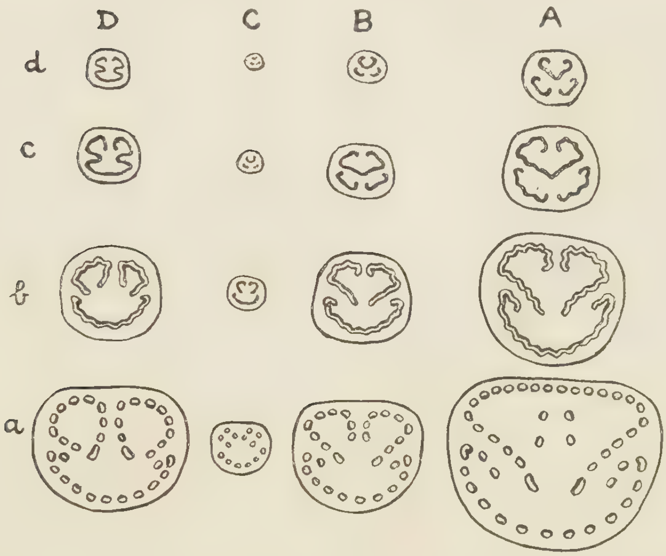

Fig. 74. The mode of arrangement of vascular strands in different parts of the leaf-axis. Each of the vertical rows (A–D) shows the different parts of a leaf, and each of the horizontal rows (a–d) shows the same regions in different leaf-axes. $(\times \frac{2}{3})$

A row, The most advanced type of the Cyatheeae (e. g. *Al. Bongardiana*)
B row, The intermediate type of the Cyatheeae (e. g. *Al. podophylla*)
C row, The simplest type of the Cyatheeae (e. g. *Al. formosana*)
D row, The type of *Cib. Barometz*
a row, Basal part of the petiole
b row, Middle part of the petiole
c row, Upper part of the petiole
d row, Middle part of the rachis

margins, and at the same time, those of the superior series connect each other so as to form a Γ7-shaped band, the longer arm of which is derived from the laterally projecting strands, and the shorter one from those projecting upwards (Fig. 74, b row). When the superior projecting strands are not completely isolated, as in the case of the young plant, or of *Al. acaulis* and *A. podophylla,* they are connected, in their original position, with the median upper part of the superior arc (Fig. 74, b C, b B). When they are completely isolated as in *Cya. spinulosa, Al. Bongardiana* and *Al. latebrosa,* the central part of the upper arc is separated, and the new margins thus formed curve inwards and connect with the isolated strand, so as to form the shorter arm of the Γ7-formed band (Fig. 74, b A). The completion of the formation of the three wavy bands, two superior and one inferior, takes place in various parts of the petiole, but generally, it occurs near the middle part of the petiole. In the petiole of *Al. acaulis* and *Al. formosana* and of the young plants of other species, three

wavy bande are also formed in the same way, but as the original strands are few in number, the connected bands are small and simple (Fig. 74, b C).

Proceeding upwards, the size of the petiole as well as of the vascular bands becomes smaller, and the number of waves in each band diminishes. At the same time, the form and arrangement of the bands undergo a change. The laterally projecting parts of the superior series, i. e. the longer arms of the Γ7-shaped bands elongate, and approach each other in the median line, and at last, both ends fuse together, so as to form a V-shaped band of the superior series. Meanwhile, the inferior band is separated at the median line into two halves (Fig. 74, c row). The position where these three bands are established is usually the upper part of the petiole, or the lower part of the rachis. Proceeding still further upwards, the two separated inferior bands fuse again into one band (Fig. 74, d row). This form is found up to the very top of the rachis.

Throughout the petiole and rachis, the interconnection of the vascular strands takes place in the superior and inferior series respectively, but the two series do not connect with each other until they reach the very end of the rachis. This is the most characteristic feature, and the division of the petiolar strands into two series, which was first proposed by Thomae, seems to be justified.

Next, the transformation of vascular strands in the petiole and rachis of *Cib. Barometz* will be considered, in comparison with that of the Cyatheeae. At the base of the petiole, not far from the very base, separate strands begin to connect with each other. In the petiole, the region with separate strands is very short, for nearly all parts of the petiole and rachis have the connected vascular strand. The interconnection of the strands takes place in the same manner as in the Cyatheeae, that is, the superior strands connect with each other in two bands, each in a Γ7-shape, and the inferior ones in a semicircular shape (Fig. 74, b D). This state with three bands is found, for a very short distance, at the petiolar base. At the middle part of the petiole, the margins of the bands of both series become connected laterally, thus forming a single continuous petiolar band (Fig. 74, c D). This form is maintained up to the very top of the rachis. The connected band has a heart-shaped outline opened at the upper side, both margins curving inwards deeply, and the groove on each side is derived from the connected part of the incurved margins of the superior and inferior series. Higher up, the size of the vascular band decreases gradually, and at the

same time, the number of waves diminishes, but no essential change takes place in its outline (Fig. 74, d D). The lateral grooves deepen gradually, perhaps, corresponding to the deepening of the laterally projecting strands of the Cyatheeae. In the latter, a pair of the upper row of the lateral projections join each other, but in this species the lateral grooves are not joined with each other, and remain unconnected.

THE PINNA. The pinna-axes, borne on both sides of the rachis, vary in size at different parts of the rachis. The size and arrangement of the vascular bundles at the bases of the pinna-axes in various parts also vary, and the bundles of the pinna-axes in the lower part of the rachis are more complicated than those in its upper part. In all cases, the bundles are of a type similar to those found in the upper part of the rachis, that is, there are three or four vascular bands in the larger pinna-axis, and two or three in the smaller one. Even in the largest pinna-axis, more than four strands are not found. As the pinna-axis with four bands nears its end, the upper two bands connect in a V-shaped band, and the lower two also fuse into a curved band, and this type with two bands is maintained up to the end of the axis. In the young leaves and in the leaves of *Al. acaulis* and *Al. formosana*, the vascular strands in the pinna-axis consist of two bands. Thus, in all cases of the Cyatheeae, the pinna-axes have two series of bundles, superior and inferior, which are quite independent of each other, as in the petiolar bundles.

In *Cib. Barometz*, as the rachis-bundle consists of a single band, the pinna-axes borne on the rachis have vascular bundles consisting of a single band, just as found in the upper part of the rachis.

THE PINNA-TRACE. The mode of parting of pinna-traces from the rachis-bundles must now be considered. The parts of rachis-bundles at the lateral corners belonging to both series bulge out, and then are constricted off, each in an arc or a ring-shape. This process takes place in the same way in the Cyatheeae and *Cib. Barometz.* In the Cyatheeae, the detached traces are separated from each other, and are arranged vertically. If the traces bifurcate in the main line of the pinna-axis, three or four bundles may be formed. Thus, the superior and inferior strands of the pinna-axis are direct continuations of the superior and inferior strands of the rachis. At the base of the pinna-traces, however, there appears a small strand which connects the two series; a part of the upper side of the inferior trace is separated and goes upwards, and fuses with the lower side of the superior trace. This commissural strand is short and minute, and it is often overlooked.

When the pinna-traces are small, consisting of two, they approach each other, and are connected by a commissural strand in an 8-shape, which is soon separated into the superior and inferior traces.

In *Cib. Barometz*, the two constricted traces connect in an 8-shape, which is transformed to form an opened heart-shaped pinna-trace. In this case, the connection of the two traces in the 8-shape corresponds to the same process in the Cyatheeae, but the behavior of the traces after their parting differs in the two cases. According to BOWER (1912), the mode of parting of pinna-traces of *Lophosoria pruinata* (*Alsophila quadripinnata*) is similar to that of *Cibotium*.

The mode of parting of pinna-traces in the Cyatheaceae is of the so-called extra-marginal type of DAVIE (1918).

M. THE ROOT AND THE ROOT–TRACE

The roots of the Cyatheaceae are adventitious as is usual in ferns, but as the stem takes the tree-form, they show characteristic features not seen in other ferns. Most of the ferns, especially of the Polypodiaceae, have creeping rhizomes, and the roots borne on them are short and few, while in some ferns with erect stems, the height is not great, so that the roots are also short. In any case, the roots are borne all around the stem radially, and even in creeping rhizomes, they are also borne radially, though externally they show a dorsiventral appearance.

In the Cyatheaceae, the species with creeping rhizomes, *Al. acaulis*, *Al. formosana* and *Cib. Barometz*, have a root-system similar to that of the creeping Polypodiaceae, while the roots of the species with erect stems are borne not only on the subterranean part of the stem but also on the part above the ground. The roots of the Cyatheaceae are given off from the lower parts of the petioles ; this relation is clearly seen in the species with leaf-scars on the stem surface, such as *Al. Bongardiana* and *Al. latebrosa*. In the stem with crowded leaves, however, the areas from which the roots spring are confused with one another, so that relation of the roots to the stem is not clear. The roots which are borne on the basal parts of the stem enter the ground, while those borne on the higher parts of the stem do not always reach its surface. Tracing the stem upwards, the number of the roots is seen to diminish gradually, until on the higher part no roots are found. In the young plant, the pointed basal tip of the stem is completely covered with roots. In keeping with the growth of the stem, new roots cover the older ones, and the root-mass grows larger and larger in a conical form broadening

downwards (Fig. 71). In this case, most of the roots do not reach the ground, but the mass serves as a support to the stem. The height and size of the root-mass vary, but in general, the mass is larger and higher in plants with higher and stouter stems. The largest root-mass observed by the writer was that of a specimen of *Al. latebrosa* from Formosa, in which the mass reached the height of 3 m., with a circumference of 175 cm., or average diameter of 56 cm., though the stem included within it was only 13 cm. in diameter. The roots in the mass anastomose.

The parting of the root-traces from the stem-stele has a definite relative position. They part from the stelar margin at the lateral and lower sides of the leaf-gap, or from the very bases of the parted leaf-traces, and penetrate through the cortex obliquely downwards.

N. Branching of the Stem and Adventitious Buds

The stem of the Cyatheaceae is usually straight, but the occasional branching of the stem, the formation of small branches and the existence of adventitious buds have been observed by certain authors. The branching of the stem was described by Scott (1874) in *Al. latebrosa, Al. ornata* and *Al. gigantea*, by Schoute (1906) in *Hem. latebrosa* and *Hem. Junghnuiana* and by Bower (1912, 13) in *Cya. dealbata* and *Dick. Barometz.* The formation of adventitious buds was recorded by Scott (1874) in *Al. glabra* and *Al. comosa*, by Schoute (1906) in *Hem. crenulata* and by Bower (1912) in *Al. quadripinnata.* But, the real nature of the branching and bud-formation is mostly unknown.

In the Cyatheaceae observed by the writer, true branching has not been found, but the formation of adventitious buds has been recognized in *Al. Ogurae, Al. formosana, Al. podophylla. Cya. spinulosa*[1] and *Cib. Barometz.* The nature of the buds in the four former species differ from that in the one last named. In the former four, the buds are small and bear many leaves, thus appearing like young plants, while in the last species the buds are conical processes on the stem bearing no unfolded leaves. The difference of these two types lies in the presence or absence of leaves, but that is not the absolute difference between them. The buds of *Al. podophylla* reach a length of 2 cm.

The absolute difference between these two types lies rather in the internal structure of the buds. In the very base of the bud, the stele is protostelic. Proceeding upwards, the protostele changes into a soleno-

1) A material collected by Mr. Sasaki at Botel-Tabago, an island south-east of Formosa.

stele and then into a dictyostele, after which the stelar ring increases in diameter. In the bud of the Cyatheeae, the brown sclerenchymatous sheath is found on both sides of the stelar ring. The difference of the two types is in the relation between the stelar systems of the bud and the stem. There are two types; in the one there is a vascular connection between the stem-stele and the bud-stele, while in the other there is no such connection. In the former case, a part of the stem-stele elongates outwards, and enters the bud, in which it broadens in the way just described. In this case, the bud has the nature of a branch, but the parting of the stelar branch does not cause an interruption of the stem-stele, that is, it does not make the branch-gap. In this respect, a bud of this type cannot be a true branch, for the parting of a branch always forms a branch-gap in the stelar ring. This type is found in *Cib. Barometz* (p. 274, Fig. 57). In the second type, the basal part of the bud-stele broadens within the cortex of the stem, but has no relation to the stem-stele. A bud of this type, therefore, has not the complete nature of a branch. This type is found in four species of the Cyatheeae (p. 297, Fig. 68).

O. Histological Structure of the Stem

The Epidermis and the Hair. The external layer of the stem elongates usually to form scaly hairs, so that the epidermal layer is hardly recognized as a distinct layer. The hairs of the Cyatheeae are scaly, but those of *Cib. Barometz* are always filiform. The epidermal layer and some external layers beneath it often peel off, and the exposed surface is not always the epidermis. The falling off of the epidermal layer takes place usually in the stem weathered, and in the non-weathered parts the epidermal layer is commonly preserved.

The Hypodermis. Beneath the epidermal layer of the stem, there is a layer of a brown colour, usually 1–2 mm. in thickness. This layer, the hypodermis, consists of two kinds of tissues; the outer one, situated under the epidermis, consists of large thin-walled parenchymatous cells, and the inner one of thick-walled fibers. Both tissues are about equal in thickness, and the transition between them is gradual, while at the innermost boundary of the fibrons tissue, there is a layer of cubical cells, with a thick membrane on the sclerenchymatous side, and a thin one on the parenchymatous side. The presence of this peculiar layer, i. e. "cubical cells" of the writer (p. 176), was noted by Payen and Treub in some plants. According to them, this tissue is formed by

separated processes of the elongated cells.

When the external surface of the stem peels off, the separation occurs at the middle part of the parenchymatous layer.

On the surface of the stem at the leaf-gap, there is a brown sheath resembling the hypodermal layer, but this sheath is quite different from the latter. This part is, before the falling of the leaf, a part of the fundamental tissue of the stem consisting of normal parenchyma, but at the time of leaf-fall there appears a separating layer, which is formed, however, by a change in the cell-walls, and not by a cell-formation. The cork-tissue is not found in that part.

THE CORTEX. The cortex consists of whitish parenchyma, in which mucilage sacs are embeded in the Cyatheeae, but are wanting in *Cib. Barometz.* These sacs are elongated longitudinally and contain some mucilage. They are distributed uniformly in the cortex and also in the pith. The sclerenchymatous sheath surrounding the meristele is composed of sclerenchymatous fibers. They are typical thick-walled elements. At the boundary between the sheath and the fundamental parenchyma there is a peculiar layer of the cubical cells just described.

The cork-tissue is not found in the cortical tissue, but it was found in damaged fundamental tissue of a stem of *Al. formosana* from Okinawa Island.

THE STELE. The stele of the Cyatheaceae is constructed after the typical fern-type, i. e. the amphicribral concentric type. The xylem occupies the central part of the stele, and consists of tracheids and parenchyma. The tracheids are all scalariform, and no protoxylem is found. The phloem is situated on both sides of the xylem. On the inner side of the phloem, there is a row of sieve-tubes, which can be distinguished from other elements by their larger size. On the external side of the phloem, there is a layer of the protophloem, in contact with the inner side of which a peculiar layer is present. The elements of this layer have the size of sieve-tubes, but usually lie horizontally, so that in a cross section of the stem, they are elongated tangentially, and have been described as "tangential cells" (p. 211). Similar elements were also found by ZENETTI (1895) in *Osmunda* and named 'Quergestrecktezelle'. In some cases, at the position of this layer, longitudinally elongated cells are found, which have been described as "mucilage cells" (p. 177). The presence of such elements were also described by SCHÜTZE (1906) in some Cyatheaceae under the name 'Sekretzelle'. The writer has found elements of the latter type in *Cya. spinulosa.* In some plants, both kinds of elements, cells elongated longitudinally and tangentially.

are found together in one layer. Thus, these two kinds of elements must be the same, the only difference being in the directions of the cells, either vertical or horizontal. There are also elements which run obliquely. This tissue is found also in *Cib. Barometz.* The protophloem is usually flattened, and is separated from the endodermis by two or three layers of pericyclic cells.

The Pith. The pith consists of whitish parenchyma, and its histological structure is quite the same as that of the cortex. The construction of the mucilage sacs and the sclerenchymatous sheaths is also the same.

The Medullary Bundle. The medullary bundle is a thin long strand running longitudinally through the pith. It has the same thickness throughout the length, but it has a tendency to thicken a little at its upper end.

It is constructed according to the protostelic type, and is enclosed in a distinct endodermis. In smaller example, the xylem consists of a tracheidal mass, and in that somewhat larger, the tracheidal mass includes a parenchymatous pith, while in the largest, the central parenchyma becomes so large as to include a cavity. In any case, the phloem encloses the xylem, and internal phloem is never found. In most of the species, medullary bundles are of the first or second type, but in *Al. Bongardiana, Al. latebrosa* and *Cya. spinulosa,* the third type is also found. In all cases the position of the protoxylem is endarch. In the phloem, neither vertically nor tangentially elongated cells are found.

The sclerenchymatous sheath which encloses the medullary bundle consists of sclerenchymatous fibers similar to those of the sheath of the meristele, and at the boundary between this sheath and the fundamental tissue there is a distinct layer of cubical cells.

The Cortical Bundle. The histological structure of the cortical bundle is quite similar to that of the medullary bundle. The bundle shows three types of xylem-structure as in the medullary bundle.

P. Histological Structure of the Leaf

The petiole and the rachis show the same histological structure.

The Epidermis. The epidermis of the petiole and the rachis is an external cell-layer. Beneath the epidermis, is a parenchymatous layer, some cells thick, which passes inwards to the sclerenchymatous hypodermis, which is composed of fibrous elements. In the young stage, the surface of the petiole is covered with scales, which are gradually

cast off. In *Cib. Barometz*, filiform hairs are found instead of scales. Wen-like or spiny processes, found on the surface of the petiole, are stout, consisting of thick-walled cells, which contain no vascular system.

THE LENTICELS. Throughout the petiole and rachis, lenticels are found on each of the lateral sides. They are grooves containing loosely arranged cells, and no cambial layer is formed, so that when the cells within them fall out, they remain empty.

THE FUNDAMENTAL TISSUE. The fundamental tissue of the petiole and the rachis consists of whitish parenchyma. At the boundary between this tissue and the hypodermal layer, no peculiar layer of cubical cells is found. In the Cyatheeae, a small amount of mucilage cells is found, but they are absent in *Cib. Barometz*. Outside the vascular bundle, no brown sclerenchymatous sheath is found, but in contact with the external side of the endodermal layer, there is always a whitish fibrous sheath. It surrounds the strand, and is composed of fibers.

THE VASCULAR BUNDLE. The form of the vascular strands differs in that, some are separate while some are combined in wavy form, but in their histological structure there is no essential difference. Each of the separate bundles has a V- or semicircular shape, and is constructed according to the concentric type. In the center there is a V-shaped xylem, consisting of one or two rows of tracheids, and the protoxylem is found on the inner side of the median curved corner. The phloem surrounds the xylem, and is of the almost uniform thickness, but on the inside of the xylem-arc it is somewhat thicker. Consequently in some cases, especially in small strands, the phloem occupies the internal groove of the xylem, so that the outline of the phloem and the endodermis becomes semicircular. On the external side of the phloem, is a layer of the protophloem, which is very distinct on the outer side of the xylem-arc, but is indistinct on the inner side. In contact with the protoxylem, there is a cavity, the so-called protoxylem-cavity, in which tylosis-parenchyma is sometimes found. This latter is found usually in the largest strands. In the phloem of the petiole, there is no peculiar row of tangentially or longitudinally elongated cells, such as is found in the stem.

In the combined bundle of the petiole and the rachis, the corresponding tissues of the neighbouring strands connect with each other, so that the central xylem and the phloem on both sides combine in a wavy form.

THE LEAF-TRACE. The protoxylem and its accompanying cavity

in the petiolar bundle are established at the time when the bundle is detached from the stem-stele as the leaf-trace. In the stem-stele, there is no protoxylem. On the inner side of the stelar margin at the leaf-gap, the protoxylem makes its appearance. The marginal part is then separated as a leaf-trace, and the protoxylem thus formed becomes the protoxylem of the leaf-trace. In the leaf-trace in connection with the medullary or cortical bundle, the protoxylem of the bundle becomes the protoxylem of the leaf-trace. In any case, at the stelar margin, the peculiar layer of tangentially or longitudinally elongated cells disappears, so that they are not found in the leaf-trace nor in the petiolar bundle.

The Lamina. The lamina is thin consisting of several layers of assimilating parenchyma. The epidermis consists of the wavy cells usually found in ferns. Stomata are found only in the lower side of the lamina.

Q. Histological Structure of the Root

On the histological structure of the root, no particular points were found. In older roots, the external tissue is crushed, but in the younger ones, the surface is covered with root-hairs.

The epidermis and the cortex are brown. The latter is very thick and consists of two parts, the outer composed of thin-walled parenchyma, and the inner of thick-walled fibrous elements. The stele is small and consists of a diarch bundle. Some cases with triarch and tetrach bundles have been described in some Cyatheacean roots (De Bary, 1877; Schütze, 1906), but the writer has never met with such instances; they have always had diarch bundles.

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